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INTRODUCTION

This special issue of the International Journal of Comparative Psychology presents some of the papers on perception and cognition given at a symposium sponsored by the I.J.C.P. at the XXIVth International Congress of Psychology at Sydney, Australia, 1988. These papers on a variety of species are unified by a common theme—the attempt to understand basic behavioral processes within an evolutionary framework. These papers follow the tradition of comparative psychology in that the behaviors of different species are studied in the attempt to provide a broad understanding of the interdependent processes of perception and cognition, an understanding that is based on those aspects that are common to and those that are unique to different species.

A fundamental problem of perception—depth and distance perception—is addressed by the first two papers. McFadden (Australia) presents an analysis of depth and distance perception in the pigeon from the point of view of "eye design", a design constrained by the physical properties of the spatial array. Greenberg (USA) shows how differences in the environment may affect depth and distance perception in two closely related rodents (gerbils and spiny mice).

The other three papers focus upon problems of scaling, categorization and identification of environmental stimuli. Eisler (Sweden) provides scaling data for rats and humans suggestive of a "knowing before doing" principle for both species. Zoeke, Sarris, and Hofer (West Germany) compare three types of psychophysical context effects in birds and humans. Two of these effects, range and distribution of test stimuli, appear to reflect a basic perceptual factor invariant across species, while the third, presentation frequency, is most strongly evident in the performance of adult humans. Chase and Heinemann (USA) present some comparative data along with a theoretical account of identification and categorization performance.

In sum, this special issue on perception and cognition points to at least three fruitful aspects of comparative research: the analysis of convergent functions, the investigation of species-environment interactions, and finally, the experimental testing of specific models and theories.

Sheila Chase and Barbara Zoeke

EYE DESIGN FOR DEPTH AND DISTANCE PERCEPTION IN THE PIGEON: AN OBSERVER ORIENTATED PERSPECTIVE

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ABSTRACT: The perception of the distance of objects with respect to an observer (egocentric distance) and the perception of the relative distance (depth) between external points was found to be optimised in the pigeon visual system according to the optical and retinal constraints of the eye. Each of these perceptual capacities is mediated by different binocular mechanisms in the frontal field, both of which appear to be designed for a stationary world. This is particularly evident in the egocentric distance estimation that occurs during the reaching movement when pecking. Here both the saccadic nature of the head movement and the convergence eye movements appear to allow constant retinal stimulation. This system of vergence signal alone is inadequate for depth perception which is instead mediated by retinal disparity. Stereopsis in the pigeon appears to be more effective for pattern decoding than for absolute spatial perception.

Any system faced with interpreting the relative position of objects in space must do so within a frame of reference. Thus, the perception of the relative distances between external points (depth perception) must interact with the observer orientated perceived egocentric distance of those objects (distance perception).

The distinction between depth and distance perception is important, as their interrelationship will only be attained through knowledge of the mechanisms underlying each capacity. The current popular literature on spatial perception has emphasized the role of depth information as a major linking feature in visual perception (Barlow, 1981) or an independent channel of visual processing in mammalian and primate systems (Livingston & Hubel, 1987). Physiologically, this scheme is based primarily on retinal disparity as the underlying mechanism of stereopsis (Hubel & Livingston, 1987). However as Foley (1980) has pointed out, retinal disparity alone cannot tend the true perception of the metric of visual space from an observer perspective. This is all the more so when one considers the limited range of

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stereopsis (less than 450 meters in man) and paradoxically by impli-
cation, its relevance to close range observer orientated activity.

Interestingly, birds also have the capacity for stereopsis. Neurons
responsive to horizontal retinal disparity have been recorded in the
owl (Pettigrew & Konishi, 1976) and kestrel (Pettigrew, 1979; see
also Fox, Lehmkuhle & Bush, 1977). More recently, using behav-
ioural psychophysics we have demonstrated the presence of a binocu-
lar depth mechanism in the pigeon. This mechanism appears inde-
pendent of absolute distance (McFadden & Wild, 1986) and allows
very fine acuity (McFadden, 1987).

Thus stereopsis or at least local stereopsis, is not restricted to
mammals, primates or even predatory type species as suggested long
ago by Ramon-y-Cajal (1899) and by Elliot Smith (1928, 1930) and his
school. Nor can it be said to have evolved along with increased fron-
tality as has been repeatedly claimed (Johnson, 1901; Le-Gros Clarke,
1962; Bishop, 1981).

Hughes (1977) argues that binocular vision is at least universal
among mammals, and stereoscopy not justifiably regarded as absent
from any mammal possessing a binocular field. Fox (1978) takes this
view further in proposing his proletarian hypothesis in which he pro-
poses that stereopsis is not an emergent capacity bestowed on a rela-
tively small number of elite animals, but may be a fundamental at-
tribute of vertebrate vision.

Given that stereopsis does not give a direct useful measure of the
distance of objects with respect to the observer, one could speculate
that it serves primarily as a pattern decoder aiding in accurate object
recognition. This view would thus ascribe the evolution of stereopsis
in terms of common fundamental attributes of the visual world,
rather than peculiarities associated with particular lifestyles and
their related pressures.

How local stereopsis may contribute to spatial perception in the
pigeon requires a thorough understanding of the dynamics of avian
visual processing capability (both optically and neurally) within dif-
ferent sectors of visual space. Such information can be gained by mea-
suring the static extent of the cyclopean and binocular retinal fields
and relating this to eye-movements and fixation capacity; determin-
ing the areas of visual space surveyed by the various retinal spe-
cialisations; determining the refractive properties of the eye for dif-
ferent directions of visual space in the context of the range of
accommodation, and through the use of behavioural psychophysics,
determining the capabilities of information processing in different
sectors of the visual arena.

This paper attempts to examine each of the above approaches as
applied to the pigeon visual system and in particular, with respect to

mechanisms which allow the accurate perception of the position of objects in space with respect to either an arbitrary fixation point (depth perception) or the animal itself (absolute distance perception).

1. THE BINOCULAR FIELD OF THE PIGEON

There is no dispute regarding the presence of binocular overlap within the visual field in the pigeon, however there has been much discussion over the absolute size and position of this binocular field.

To define a binocular field, one must do so in terms of a fixation plane as the absolute size of the binocular field will increase as the distance from the eye to the fixation point decreases. For this reason, binocular fields are normally defined in terms of the straight forward position, in which the visual axes of the two eyes are parallel. In the human, this means that both fovea are fixated on a point at infinite distance relate to the interocular separation.

In the pigeon, the angle between the two foveae is approximately 135° due to the lateral placement of the eyes. Therefore, it is extremely unlikely that the eyes could converge the 60-70° necessary to allow the two foveae to simultaneously observe a point in space. That is, the two lateral foveal axes cannot intersect.

However, the pigeon has a retinal specialisation in the temporal retina called the area dorsalis (Galifret, 1968). Thus, the straight forward position in the pigeon we define as when the two frontal visual axes, corresponding to the direction of the area dorsalis, are parallel (Figure 1). We have measured the binocular field with reference to this primary eye position (McFadden & Reymond, 1985).

The dimensions of the binocular field have been also measured by others for various fixation positions either using optical criterion by determining the point in the nasal visual field at which the pupil slit just approaches zero width, (Martinoya, Rey & Bloch, 1981; Jahnke, 1984) or on retinal based criterion. In the retinal mapping technique, the edge of the retinal binocular field is determined by mapping the points in the nasal visual field at which a bright light shone into the eye just fails to elicit a retinal reflex (Martin & Young, 1983; McFadden & Reymond, 1985).

It would be expected that the studies based on pupil appearance would predict a larger binocular field than the retinal reflex studies as the extent of the retina is less than the potential offered by the optics, although in some birds this mismatch is more pronounced on the nasal margin of the eye (Martin, 1984).

The family of curves in Figure 2 shows each of the binocular fields from the studies mentioned above. It should be noted that it
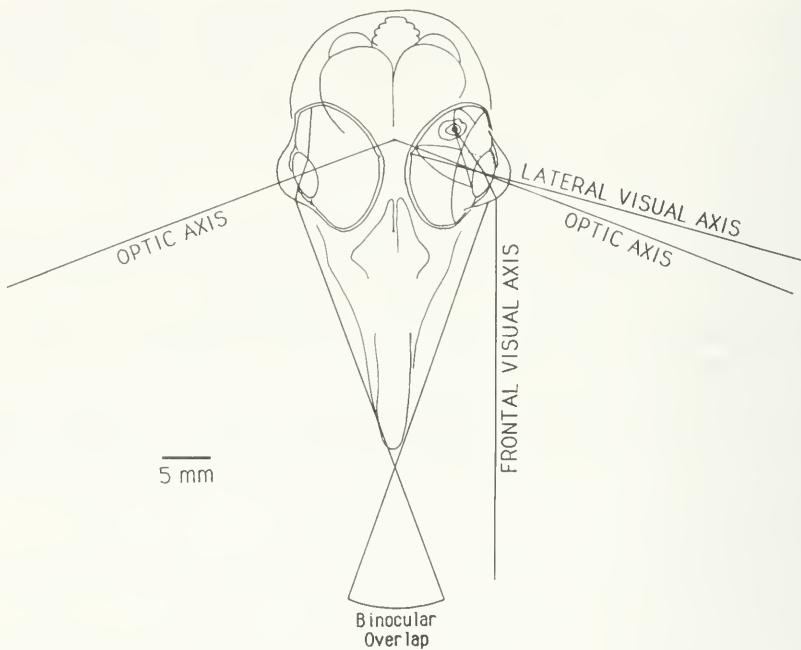
FIGURE 1. Diagrammatic view of the straightforward position in the pigeon. This is defined as when the frontal visual axes are parallel and theoretically viewing a point at infinity. The ringed dot on the retina represents the position of the area dorsalis. The fovea is represented by the depression in the retina which is intersected by the lateral visual axis.

incorporates a number of different breeds of pigeon and the techniques are based on either the optical or retinal based criterion. The optical estimates have not controlled for eye movement and are not corrected for the primary eye position. Thus the absolute size of the fields varies from study to study. Nonetheless, there is a surprising degree of similarity in terms of the overall symmetry of the binocular field with respect to the position of the beak. The peak width appears to occur at about 10° below the eye beak axis which is defined in Figure 3. Such symmetry about the eye beak axis suggests that the binocular field may be used during pecking.

Much of the discussion in the literature has centred on where maximum binocularity occurs. Thus, Martinoya et al. (1981) described the plane containing both optical axes by determining the angle at which both pupils appear to have their long axes parallel. However, this technique assumes that the eyes do not undergo vertical fixation movements with respect to the eye beak axis, and thus can-
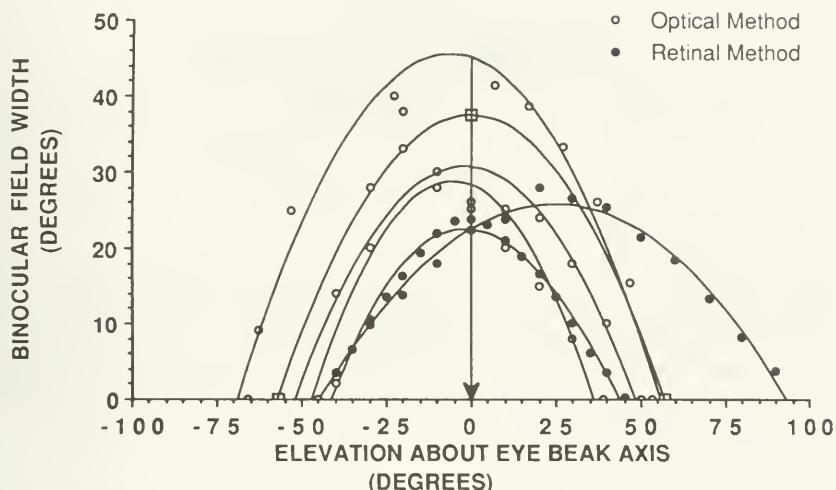
FIGURE 2. Binocular field width as a function of elevation in order from top curve to bottom are from: Martinoya et al. (1981); McFadden & Reymond (1984) corrected for the straight forward position, shown by the square symbol; the homing pigeon and blue Altenburg Trumpter from Jahnke (1984); Martin & Young (1983), rightmost curve; and McFadden & Reymond (1984) uncorrected for deviation. The arrowed line shows the eye beak axis. Data are fitted with 2nd order polynomial functions.

not effectively predict the relative position of the optical axes plane. Indeed, when the eyes are immobilised immediately following an intramuscular injection of xylazine and ketamine, the planes containing both optic axes also approximately contain the eye beak axis (Martin & Young, 1983; McFadden & Reymond, 1985).

Maximum binocularity has been also taken to mean the maximum width of the binocular field. This measure can be dependent upon whether body features such as the feathering and cere interfere with the visibility of the reflex or pupil slit. Although it cannot be denied that intrusions into the absolute field of view have functional significance, it does not allow one to determine if eye geometry alone varies between different breeds of birds as proposed by Jahnke (1984).

The measure of maximum width of the binocular field is critically dependent upon the fixation point. We have shown that the maximum retinal binocular field width is 37° when the eyes are in the straight forward position viewing an infinite fixation point.

Table 1 depicts the range of maximum widths found by various authors using retinal or optical criterion. As expected, the optical measures tend to be larger than the retinal measures (see Figure 2).
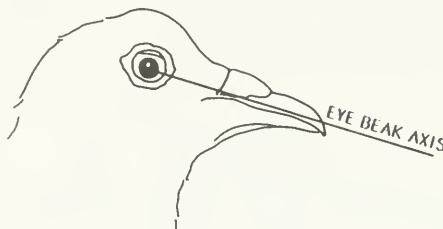
FIGURE 3. The eye beak axis lies parallel to straight edge of the upper mandible of the beak and goes through the centre of the pupil. The distance that the axis is displaced above the line of the beak is exaggerated for the purposes of illustration. However, the eye beak axis is not necessarily coincident with the line of the beak, but lies slightly above in the feral pigeon.

The latter are surprisingly consistent when the fixation point used is taken into consideration.

Thus, if a pigeon was converged for fixating an object at a viewing distance of 15 cm, the F1 distance routinely used when pecking at grain (see section 6), then the patch of ground being viewed simultaneously by both eyes would be about 9 cm in diameter. This size is presumably sufficient to allow resolution of figure from ground stereoscopically and perhaps implies that when the bird moves to F1 during pecking at patches of grain (Goodale, 1983) binocular vision is available to aid in the discrimination.

2. EYE MOVEMENTS AND BINOCULAR VISION

The pigeon has a sophisticated array of eye movements despite the tightness of the orbital fit. Nye (1969) has described small monocular eye movements resembling impulses, drifts, flashes and tremors. All are of relatively low amplitude.

Of relevance to the role of binocular vision, vergence eye movements have also been found, elicited during the peck response (Martinoya, Le Houezec & Bloch, 1984). There is no question that such eye movements will modulate the extent of the binocular field as the distance to the fixation point decreases. However, it is possible that their role is primarily to maintain an image over a constant area of the retina.

The size of the vergence eye movements elicited during pecking has been measured relative to either the maximum divergence that occurs immediately after the peck or the total convergence relative to a scotopic rest position (Bloch, Rivaud & Martinoya, 1984; McFadden,

TABLE 1
Maximum Binocular Field Widths

Max. Width	Source	Conditions
Retinal		
24°	Walls, 1942	"Upon full convergence", unspecified technique.
24.3°	Martin & Young, 1983	Under ketamine, uncorrected for drug induced deviation.
24.°	McFadden & Reymond, 1985	Under ketamine/xylazine, uncorrected for drug induced deviation.
37°	McFadden & Reymond, 1985	Straight forward position, infinite fixation point, corrected for drug induced deviation.
Optical		
42°	Martinoya et al., 1981	Unmonitored vergence state, possibly fixation on camera at 28 cm.
28-40°	Jahnke, 1984	Unmonitored vergence state, flash at 28 cm, field limited by head silhouette.

Lemeignan, Martinoya & Bloch, 1986). The scotopic rest position is the absolute constant position that the eyes adopt when a pigeon is left in the dark for 20 minutes. It is unknown whether the scotopic rest position is equivalent to either the position of the eyes immediately following death or to the straight forward position.

Relative to the scotopic rest position, vergence movements can be up to 17° in each eye. If the scotopic rest position is equivalent to the

straight forward eye position as defined in Section 1 and shown in Figure 1, then 17° of convergence in each eye would allow fixation at a distance of 3.9cm. Since the distance from the eye to the tip of the beak is about 3.7cm, at maximum convergence the object of regard would be just in front of the beak. Although each eye is independently mobile, evidence for binocular fusion is provided by the striking and precise temporal synchrony of these vergence movements. Not only does each eye converge in short bursts, but the initiation of each burst appears coordinated in time (Bloch et al. 1984). In addition, the amount of convergence is linearly related to the distance of the fixation point.

The Influence of Binocular Feedback on Convergence Eye Movements

The mechanism underlying these apparently coordinated eye movements is modulated if binocular interaction is removed either physically or neurally. Physical intervention can be induced by the placement of a binocular field occluder in front of one eye only (Figure 4). It should be noted that this technique does not produce any true blind spots in the visual field at distances beyond the beak but simply removes binocular feedback. Under these conditions, eye convergence still occurs (Martinoya et al. 1984). Figure 5 shows the data from Martinoya et al. (1984) replotted so that normal convergence can be directly compared to that which occurs when binocular feedback is blocked. It can be seen that as the eye gets closer to the grain, the amount of convergence increases linearly. However, the line of best fit under normal viewing conditions ($y = -1.99x + 32.3$) is significantly less than the regression line under conditions when binocu-
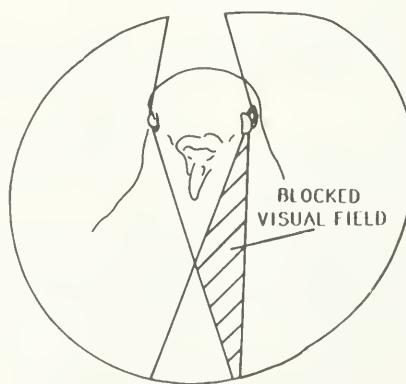
FIGURE 4. Diagrammatic representation of the effect of placing a moon shaped occluder in front of the binocular field of one eye.
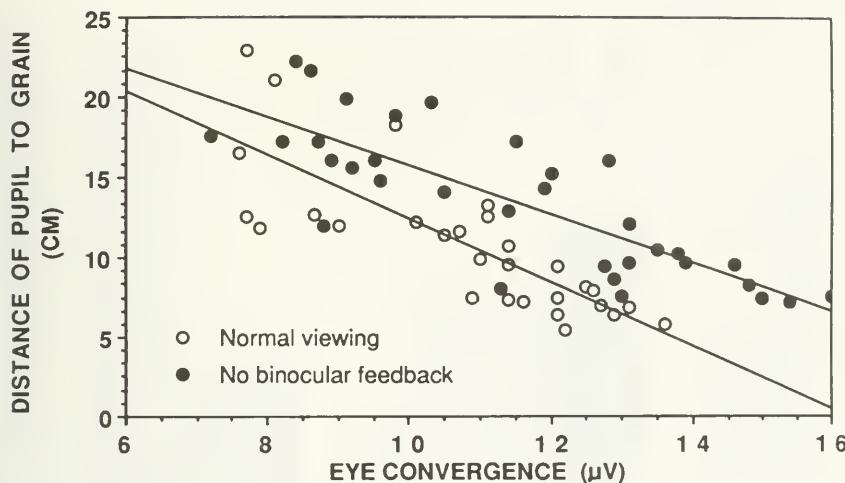
FIGURE 5. Eye convergence (μV $\times$ 10^{-2}) plotted as a function of distance while pecking at a single grain. Data taken from Martinoya et al. (1984) and fitted with regression lines.

lar feedback is blocked (y = −1.5x + 30.84) (Analysis of Covariance; $F = 15.8$; df = 1,60; $p < .01$). Deprived of binocular feedback, the oculomotor system appears to over-converge as if deprived of modulatory inhibitory control.

A similar picture emerges when binocular interaction is removed neurally by the creation of a split brain preparation (McFadden et al. 1986). This technique involves cutting the major commissures that join the two half brains and measuring the vergence eye movements during pecking before and after surgery. One of the major commissures of relevance is the dorsal and ventral supraoptic decussation (DSO) which lies just above the optic chiasm. Evidence has implicated the DSO in mediating interocular transfer of pattern discriminations in the pigeon (Meier, 1971; Burkhalter & Cuenod, 1978). The DSO is also believed to help integrate binocular information in the thalmofugal pathway which is thought to be analogous to the genticulate-striate pathway in mammals and primates (Karten, Hodos, Nauta & Revin, 1973; Pettigrew & Konishi, 1976).

Figure 6 shows the change in eye convergence in 5 birds caused by cutting the DSO compared with 4 birds in which other commissures were cut, but DSO remained intact. Rather than removing convergence, the effect of creating the DSO split brain preparation was to cause an increase in convergence. The difference in amount of convergence before and after surgery was much greater in the DSO lesioned group ($t = 2.8$, df = 7, $p < .05$).
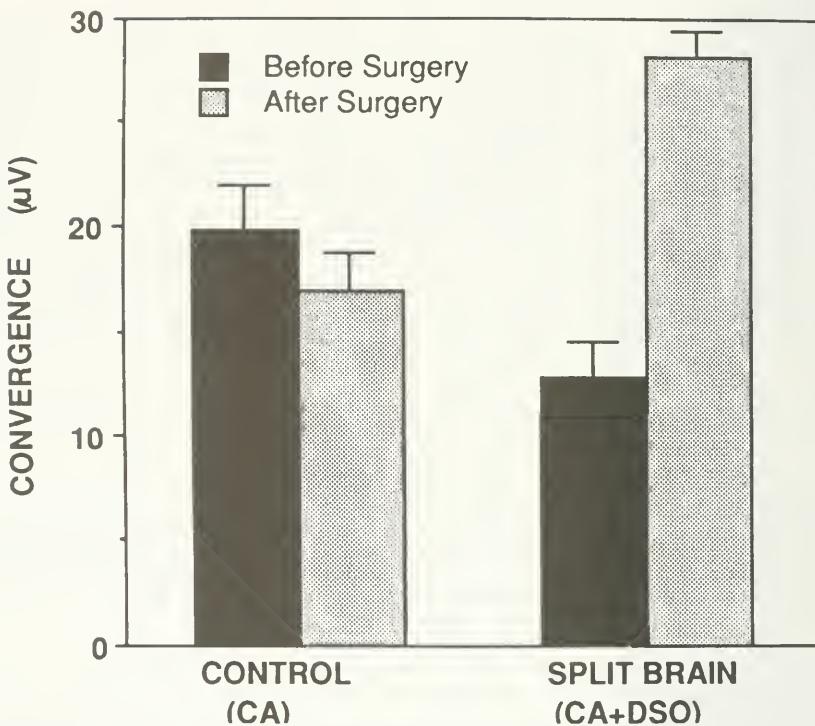
FIGURE 6. The effect of cutting the supraoptic commissure (DSO) compared with cutting the anterior commissure (CA) on eye convergence ($\mu V \times 10^{-2}$). Bars show the standard error.

Not only does interference in binocular neural integration cause an increase in convergence, but it also affects pecking accuracy. The peck error in 9 adult pigeons before and after split brain surgery is shown in Figure 7. Normally, peck accuracy decreases as seeds become large and unmanageable, but is best for smaller seeds like millet and wheat ($F = 10.6$; df $= 3,66$; $p<.01$). Pecking accuracy also decreases markedly as a result of cutting all the major commissures (anterior commissure, supraoptic commissure, tectal and posterior commissures) ($F = 9.8$; df $= 2,66$; $p<.01$). The deficits shown in Figure 7 were permanent since pecking accuracy was measured up to one year after the split brain surgery and after the birds had had much pecking practise under the new perceptual conditions.

Thus, it can be seen that eye movements in the pigeon could allow binocular fixation and possibly fusion in an area of visual space as large as $37 + 17 + 17 = 71°$ for near objects. These eye movements are disrupted when binocular feedback is inhibited either physically or neurally. Surprisingly, in both cases, convergence ap-
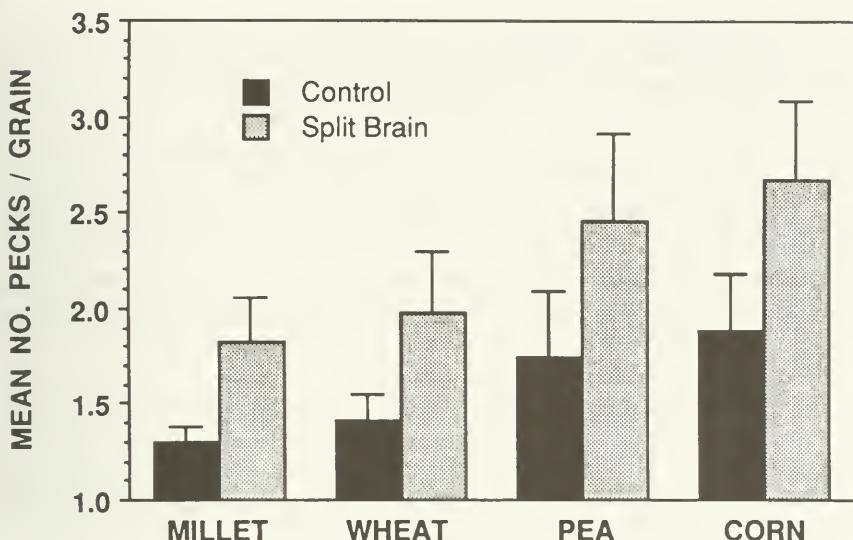
FIGURE 7. Pecking accuracy for different seed sizes before (Control) and 1 year after surgery (Split Brain) in which all the major commissures were cut. Bars show the standard error.

pears to increase as if there is dis-inhibition of vergence control. The convergence eye movements are correlated with the position of grain during the peck response. The vulnerability to interference with binocular interaction is not only seen in the vergence system but is also reflected in the accuracy of the reaching movement during pecking. Before we examine the role of the vergence system in mediating distance perception during pecking, it would be of relevance to understand the retinal and optical characteristics associated with this frontal binocular area of the pigeons visual space.

3. THE AREAS OF VISUAL SPACE SURVEYED BY THE RETINAL SPECIALIZATIONS

It has been noted since Rochon-Duvingneaud (1943) described the 'visual trident' (see Walls, 1942) that birds have the remarkable feature of two separate retinal specialisations allowing high resolution over much of the retina. These specialisations are characterized by increased cell density and in many birds (for example—hawks, eagles, kingfishers and hummingbirds) are both accompanied by foveae. The fovea is a high acuity pit within the retina (see Snyder & Miller (1978) for an interesting discussion of a possible optical advantage of the foveal pit).

In the pigeon with its laterally placed eyes, it is a central area of the retina which subserves the lateral visual field that is accompanied by a fovea. The pigeon fovea is quite deep (see pictures in Chard & Gundlach, 1938; Galifret, 1968; Clarke & Whitteridge, 1976) and more developed than in the human eye (Walls, 1942). The horizon in the plane of the foveae appears well served by an almost streak like density distribution of the displaced ganglion cells (see Fig. 3 in Hayes & Holden, 1983).

The second specialisation occurs in the superior temporal retina, and aids detection in a more frontal downward direction. The precise projection of this 'area dorsalis' as it has been called (Galifret, 1968) is in dispute and will be addressed below.

It has often been proposed that such a dual visual system offers not only the advantages of lateral detection in a panoramic system (eg. predators), but also a capacity for possible parallel processing of visual information closer at hand (e.g. during feeding) (Walls, 1942; Catania, 1964; Bloch & Martinoya, 1983).

4. LOCATION AND CHARACTERISTICS OF THE RETINAL SPECIALISATIONS

The presence of a distinct fovea in the pigeon retina has long been known. Viewed with an ophthalmoscope, the pigeon fovea appears as a bluish ring that has a dark spot in the centre and placed just up from the tip of the pecten. Due to their easy visibility to the experienced observer, the foveae can be accurately mapped in relation to their position in the visual field. The foveal axis lies close to the optic axis (within 5°). Each foveal visual axis is slightly nasal with respect to the centre of each uniocular visual field. With the eyes in the primary position we have found that the angle between the two foveal axes is 147° (see Figure 1).

It is intriguing to note that laser lesions of the central fovea in the pigeon does not have much effect on their visual acuity of grating patterns as measured behaviourally (Blough, 1973). This may be due to the use of other cell rich areas of the retina. A ganglion dense strip posterior-superior to the pecten was described by Whitteridge in 1965 (see Binggeli & Paule, 1969). The distribution of cells within the internal granular layer (nuclei of the muller fibres, horizontal, bipolar and amacrine cells) were mapped by Galifret (1968). In addition to the central area surrounding the fovea, he found the cells to be densely packed at a posterior-dorsal position which he called the area dorsalis. He also noted that the area dorsalis could be assimilated in the 'red field', an area of pigeon retina which contains a high density of red and orange oil droplets.

Staining and mapping of the ganglion cell layer also produced this characteristic distribution (Binggeli & Paule, 1969) with the area dorsalis estimated to contain $36 \times 15 \times 10^3$ cells/degree (Hayes & Holden, 1983).

The amacrine and bipolar synaptic densities do not parallel the cellular densities of the amacrine and bipolar cells, however the highest synaptic densities in the inner-plexiform layer occur in the red field, even higher than that found at the fovea (Yazulla, 1974).

Figure 8 shows the data from the various studies superimposed relative to the angle of the pecten. There is no doubt that in terms of
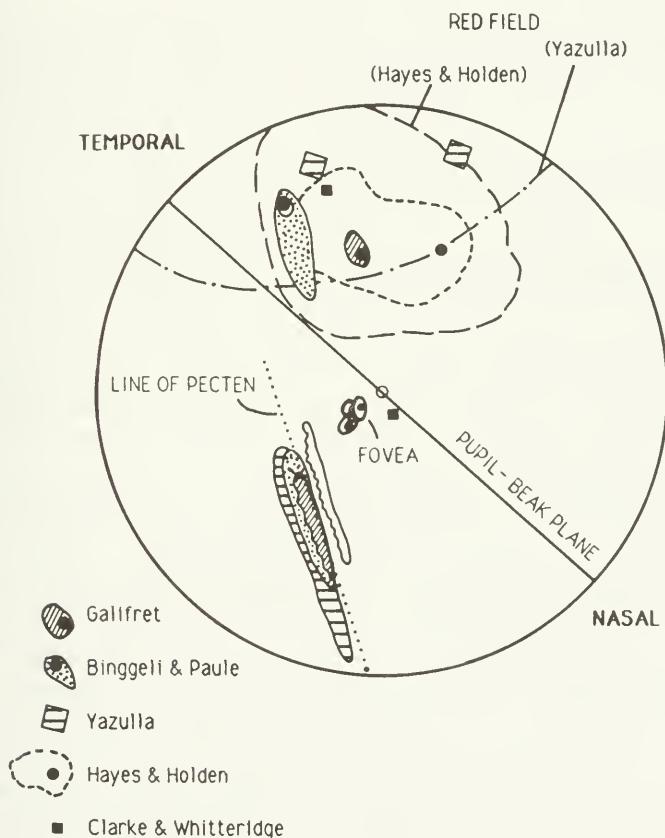
FIGURE 8. Retinal map of the combined data superimposed relative to the angle of the pecten for peak cell densities of: the internal granular layer (Galifret, 1968); ganglion cells (Binggeli & Paule, 1969; Hayes & Holden, 1983); synaptic density (Yazulla, 1974); and tectal magnification (Clarke & Whitteridge, 1976). The large dashed line and dash-dot line represent the borders of the red field found by Hayes & Holden and Yazulla respectively.

cell density, the presence of an 'area dorsalis' consistently appears in a similar retinal area. This quadrant of the retina also contains the red field, although there is no empirical evidence as to the significance, if any, of the coincidence.

The question remains as to where this area dorsalis projects within the visual field. There have been frequent suggestions that it may subserve the frontal field (Clark & Whitteridge, 1976; Galifret, 1968; Goodale, 1983; Bloch et al., 1984; McFadden & Reymond, 1985). Determining its precise projection reflects the difficulty of accurately ascertaining the projection of retinal landmarks not visible ophthalmoscopically.

Only one study has attempted to directly address this question. Hayes, Hodos, Holden & Low (1987) examined the transclearal image formed by light shone from fixed visual field positions into the eye dissected in situ in post mortem pigeons. They concluded that the area dorsalis receives input from the lower visual field (the ground) and not necessarily from within the binocular field.

In such a preparation one is faced with interpreting how the post mortem eye relates to the dynamics of a surprisingly mobile eye in real life (see Martin, 1986). One might need to consider the effects of corneal and optical degradation and the eye deviation that is concomitant with death (approximately 12° from the primary position). It is also known that each eye can converge about 15° when a bird is observing grain prior to pecking (well before F1) (Bloch et al. 1984; McFadden et al., 1986). In addition, vertical and cyclorotational eye mobility have not yet been explored.

All these concerns reflect the difficulty in relating static eye maps to the behaviourally active bird. For example, in the composite cell density maps of Gallifret (1968), Binggeli & Paule (1969), Yazulla (1974) and Hayes and Holden (1983) shown in Figure 8, the projection of the various retinal features can only be ascertained if eye position is defined. Thus in Figure 8, eye position is defined roughly with respect to the angle of the pecten (32° below the eye beak axis). The plane containing the eye beak axis is marked and shows that the superior temporal quadrant of the retina does contain some interesting attributes that lie near this plane. The centre of the binocular field at the elevation of 10° below the eye beak axis stretches 18.5° from the projection of the edge of the retina when the eyes are in the stright forward position. At full convergence, the centre of the binocular field will lie 36° from the projection of the edge of the retina. The whole retina from edge to edge encompasses 169° of visual space. This means that in Figure 8 the *centre* of the binocular field 10° above the eye beak plane will lie 38° in from the edge of the retina. This is very close to the collection of high cell density attributes in this quadrant of the retina.

5. OPTICAL CHANGES OVER THE VISUAL FIELD

The regional specialisations seen in the avian retina are also to some extent mirrored in the refractive properties and optical characteristics of the eye. Various studies have speculated or concluded that the pigeon is myopic in the frontal field and emmetropic (Nye, 1973; Bloch & Martinoya, 1983) or even hypermetropic (Catania, 1964; Millodot & Blough, 1971) in the lateral visual field.

The pigeon eye is regarded as asymmetric both in shape and refractive properties. Variation in the posterior-nodal distance (PND) can be seen in the early insitu cross-sectional drawings by Chard & Gundlach (1938) and Gundlach, Chard & Skahen (1945), when the temporal PND is smaller than the nasal retina. One may expect that modification may occur as a result of the histological process. The opposite effect has been measured in the chick retina where the PND in the horizontal visual field is consistently longer in the temporal compared to the nasal retina (see Figure 9(c) in Schaeffel, Glasser & Howland, 1988). It is possible that the PND varies as a function of elevation as well as with the nasal-temporal direction.

A trend toward myopia in the superior and nasal retina was described within a relatively central retinal area using standard retinoscopic techniques in an anaesthetized pigeon (Millodot & Blough, 1971). Using electroretinographic optometry, again in anaesthetized pigeons, and the principle of conversion of optical defocus into lateral shift of the image of a grating, Fitzke, Hayes, Hodos & Holden (1985) escape the hypermetropic artifact associated with off axis retinoscopy (Glickstein & Millodot, 1970) which would arise if variation occurs in the origin of the light reflex over different eccentricities. Fitzke et al. (1985) conclude that refractive state varies systematically between upper and lower visual field, with the eye progressing from an emmetropic state on the horizon (35° above the eye beak axis) to 5 diopters (D) myopic at more negative elevations. In the nasal to posterior retinal direction, the data indicate little refractive change ($-1D$ to $+0.5D$ respectively). Unfortunately the data was only extended to within 23° of the edge of the binocular field itself, and thus the refractive state within the binocular field was not measured.

The overall refractive state of the pigeon eye is also modulated by its accommodative capacity. Accommodation in the pigeon is mediated by the ciliary muscle which in birds is striated (Gundlach et al., 1945). Both the cornea and lens participate in the accommodative response, with the corneal component having a proportionately greater role in the lower range of accommodation (Martin, 1987; Schaeffel & Howland, 1987). Estimates of the range have varied from 12D (Gundlach et al., 1945) to 5D (Levy & Sivak, 1980).

Points in the binocular field are likely to be imaged through the

peripheral optics. It is possible that such accommodative range may not necessarily act equally at the peripheral margins of the cornea and lens, dependent on the relative rate of curvature and the structural elasticity. If such differences do exist, then it is possible that the frontal field maybe more limited in its available depth of field.

Behavioural Measures of the Near and Far Point of Accommodation

The near point of accommodation can be estimated by measuring the visual acuity of the pigeon at different viewing distances. In the frontal binocular field, visual acuity (square wave grating acuity) was best at a distance of 10 cm and became progressively poorer at greater viewing distances. In contrast, the visual acuity at a distance of 10 cm in the lateral field was 3.5 times worse than frontal acuity but improved at greater viewing distances (Bloch & Martinoya, 1982).

It is clear that differences exist between the frontal and lateral fields in terms of visual acuity measures. At least a partial role of the optics in mediating this distinction can be assumed, and the near point of accommodation in the binocular field is likely to be less than or equal to 10cm. The peck response of the pigeon indicates that the near point could be as close as 5.6 cm, as the grain is not normally observed closer than this distance. As discussed in Section 7, it appears that the far point of accommodation in the frontal field or at least the greatest distance in which stimulus control occurs for distance discrimination may be less than 20cm.

6. BINOCULAR DISTANCE PERCEPTION DURING PECKING

Birds use their feet and mandibles to reach for and manipulate objects within close visual range. In the pigeon, pecking at small grains is an accurate motor action, intimately tuned to the size and distance of the seed (Zeigler, Levitt & Levine, 1980). The peck response is stereotypical between and within individual birds, and is characterised by fast saccadic head movements interspersed with fixation stops. From the last of these fixation stops the eyes begin to close and the beak opens simultaneously, so that at the inflexion point in the peck movement the eyes are fully closed and the beak opened exactly the amount needed to effectively grasp the seed. Grasping the seed is followed by a series of backward head movements accompanied by complex manidibulation and swallowing motions.

Despite the apparent ballistic nature of parts of this pecking movement, it is irresistible to propose that distance perception aids

the accuracy of this movement and is provided by visual feedback in the early stages of the peck sequence. We have attempted to examine the validity of this hypothesis and determine the type of visual cues used. Certainly it is true to say that if visual feedback is completely blocked during the peck response, then the accuracy of this movement is very poor indeed. This is not to say that successful grasping attempts are not made by blind birds, but the low probability and learning required lead one to suggest that this may be due to reliance on recall of spatial maps.

The saccadic head movements accompanying the peck response were first noted by Smith (1974) and Hodos, Leibowitz & Bonbright (1976). We have found that in the adult trained pigeon pecking at grain, the head is moved 6.6–6.9 cm in 20-40 milliseconds. The head velocity is thus conservatively estimated at 165 cm/sec. Maintaining a steady image over a constant retinal area under these conditions may be difficult and is likely to be accompanied by retinal slip. However the flow field has yet to be modelled.

The fast saccadic head movements are also interspersed with fixation stops and have been described in detail by Goodale (1983). He found that the characteristic stereotyped responses occurred when both operantly discriminating the presence of a small black dot on a vertical key (by pecking at the dot) and when pecking at patches of mixed grain.

The absolute time spent at each of the last two stationary fixation stops (labelled F1 and F2) was between 100-200 milliseconds depending on the precise condition. This is 5-10 times longer than that spent in each movement phase, and could possibly allow enough time for visual computation of spatial attributes of the pecking scene.

In order to examine egocentic distance perception, we have chosen pecking at a single grain of millet (3mm in diameter) since the accuracy of this movement can be ascertained with more certainty than the factors controlling the behavioural response under operant conditions.

Correlation of Peck Accuracy with the Fixation Positions

The experiments were done with 6 adult birds each given 10 trials/day (1 seed/trial) for 18 successive days. Enlarged images of the right hand side lateral view were taken at a luminance of 2 log cd/m^2 through a measurement grid with a video camera with a fast shutter speed ($^1/_{1000}$ th sec). Frame by frame video analysis revealed a number of interesting attributes of the normal peck response. We had previously found that peck accuracy is poorly developed in young birds with peck accuracy starting as high as 50 pecks/grain but improving with practice (see also Graf, Balsam & Silver, 1985). In adult birds,

accuracy in the single grain 'pick-up' test also improves, even though the birds have had much natural pecking practice. The improvement over time is shown in Figure 9. The data were fitted by an exponential function of the form:

$$y = 0.4e^{-x/2.83} + 1.31$$

indicating a rate of change with a time constant (t) of 2.83 days (training sessions) and levelling off to 1.3 pecks/grain. Pecking in the pigeon is not perfect, with a residual error evident even in highly trained birds. The error rate for peck accuracy is surprisingly high at 30%. Analysis of 61 initial pecking errors revealed that 44% were due to inaccurate grasping with the tip of the beak, 36% due to pecking short of the target and only 20% due to orientation error, most of which was composed of lateral misalignment.

    As previously mentioned each peck is accompanied by a series of head fixations and in the above birds the last two stationary positions prior to contact of the beak with the grain were measured. Initially, the distance from the centre of the pupil to the grain of millet was 9.8cm at F1 (n = 60, S.D. = 1.1) and 5.68cm at the last fixation position F2 (n = 60, S.D. = 0.4). These values are very close to that found by Goodale (1983) for pecking at patches of grain. More interestingly, the absolute position of the fixation point increased as a function of
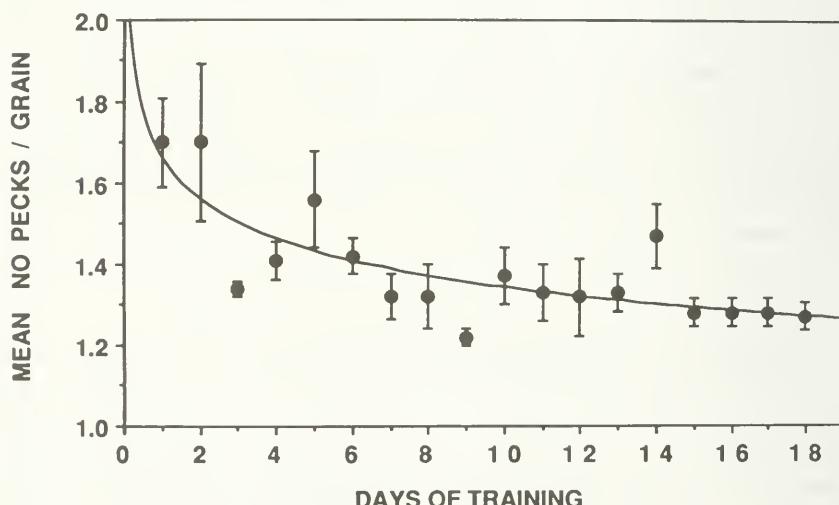
FIGURE 9. Mean improvement in pecking accuracy as a function of training (10 trial/day) in 6 adult pigeons. Bars show the standard error. Data is fitted with an exponential function.

practice. This is shown in Figure 10. Exponential fits to the data gave equations of the form:

$$y = -3.49e^{-x4.41} + 13.41 \qquad \text{for F1, and}$$

$$y = -0.97e^{-x/2.56} + 6.55 \qquad \text{for F2.}$$

Thus the final fixation positions adopted after 180 trials of training and when pecking error was minimal was F1 = 13.4cm and F2 = 6.6cm. The rate of change in pecking accuracy (t = 2.8 days) was most highly correlated with the time constant of the last fixation position F2 (t = 2.6 days) rather than F1 (t = 4.4 days). It should be noted that the variance is always less at the last fixation stop (F2) than the preceding stop (F1). However, it is the case that one or two fixation stops sometimes occur prior to F1, and it is possible that they may sometimes be included in the data if F1 is skipped. There is no question that F1 and F2 are coupled in tandem (for example, see the peaks repeated for both F-stops on days 7 and 9). The position of F1 does ultimately predict how far to move to get to F2.

These data show that the position of the head at the stationary fixation points is correlated with the accuracy of the outcome of the peck movement. Surveillance of the visual scene at F1 allows the computation of how far or for how long the head should be moved to reach F2. If F2 is not at the correct position, then the bird will generally underestimate the distance of the seed.

The Role of Binocular Feedback in Pecking

Interestingly, if binocular feedback is removed by blocking the overlap of one eye (see Figure 4), then pecking accuracy is significantly retarded ($t = 1.4$, df = 16, $p < .01$) (Figure 11). Under such conditions, the bird can eventually learn to partially overcome the effects of not having access to binocular cues. Clearly, the distance estimation is not simply based on one method but uses a variety of strategies, one of which is binocularly based.

Although the bird has difficulty in accurately grasping the target seed without binocular stimulation, examination of the stationary fixation points adopted under such partial monocular occlusion revealed a general resilience to being affected at all. Only a small but permanent decrease was often seen in the position of F1 (Figure 12A) but no change was evident at F2 (Figure 12B). This means that when deprived of binocular vision the target was often viewed at a closer distance during the early components of the peck movement.

The short peck often seen under conditions in which binocular stimulation is removed is an obvious feature if the target is viewed
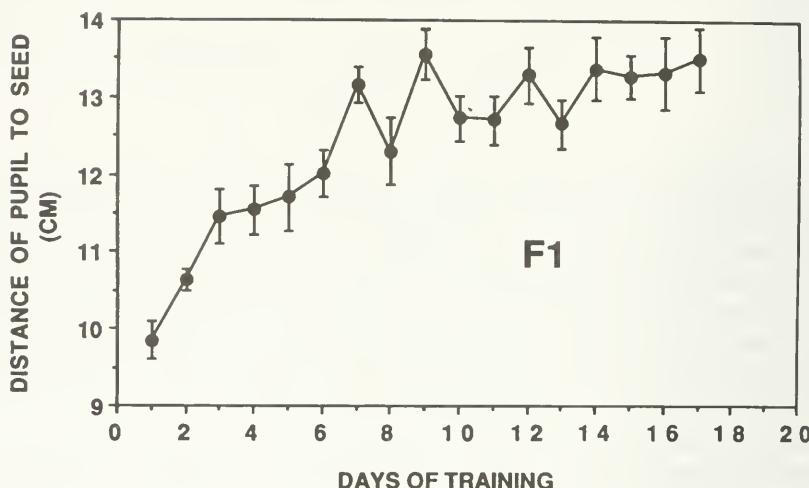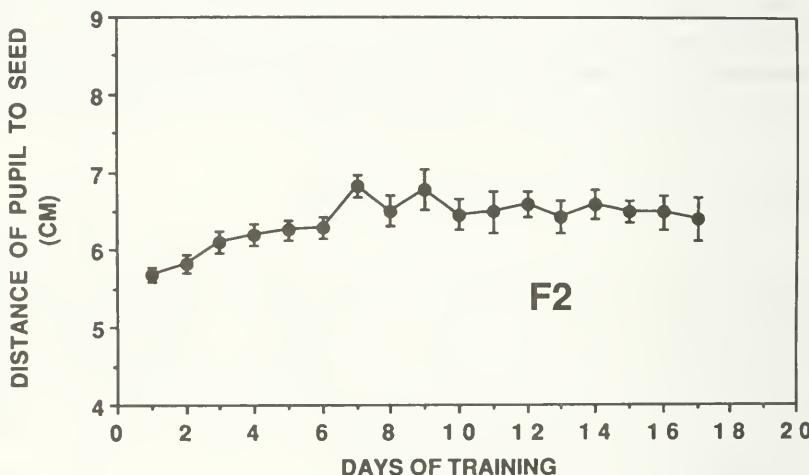
FIGURE 10. The mean fixation positions adopted by 6 birds when pecking at a single grain of millet as a function of amount of practice at: (A) the initial fixation position F1; and (B) the final fixation position F2. Standard error bars are shown.

through prisms (Figure 13). Here the virtual image is closer than the real image of the seed, and the bird uses the fused binocular image rather than the monocular image through each prism. If the bird was not using the fused binocular image then pecking would have been at
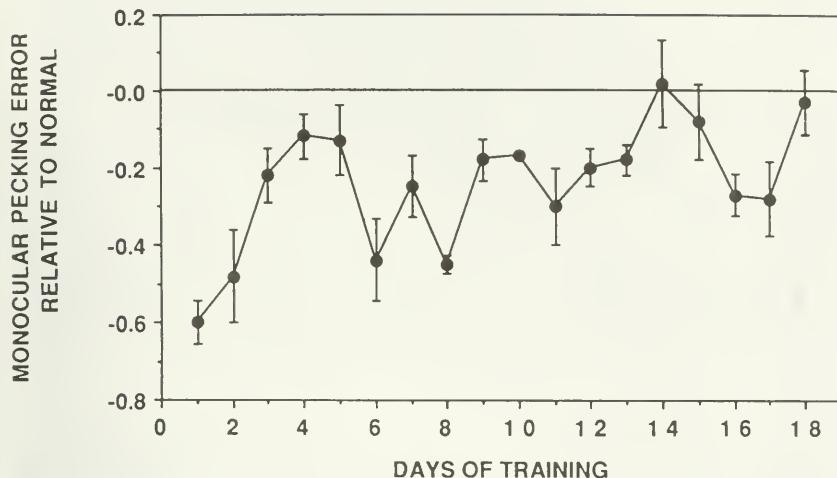
FIGURE 11. Mean difference in the pecking error for 6 birds between normal viewing conditions and conditions of monocular occlusion in which the binocular field of one eye was blocked. The eye chosen for occlusion was left in half of the birds and right in the remainder. Data falling below the line marked as -0.0 shows the increase in pecking error due to occlusion. Bars show the standard error.

the correct depth but displaced laterally. Interestingly, adaption to the prisms does eventually occur.

It is clear that distance perception is employed during the peck movement. It is also true that the seed is preferentially imaged binocularly at distances of approximately 10cm. As previously mentioned, the convergent eye movements which accompany the peck movement could result in maintaining constant retinal stimulation of the object being fixated at the stationary F-stops. The amount of convergence elicited at a fixation point could act as the means to compute the travel distance required to get to F2, the last strike position.

Such a mechanism is also used by the praying mantis to strike at moving prey with its forelimbs (Rossel, 1983). Like the pigeon pecking at grain, the mantis computes the equivalent of the convergence angle between the two eyes and uses it to estimate the egocentric distance to the prey object.

7. BINOCULAR DEPTH PERCEPTION

Relating the position of a point in space to an egocentric body position is quite different to perceiving the world in three dimensions
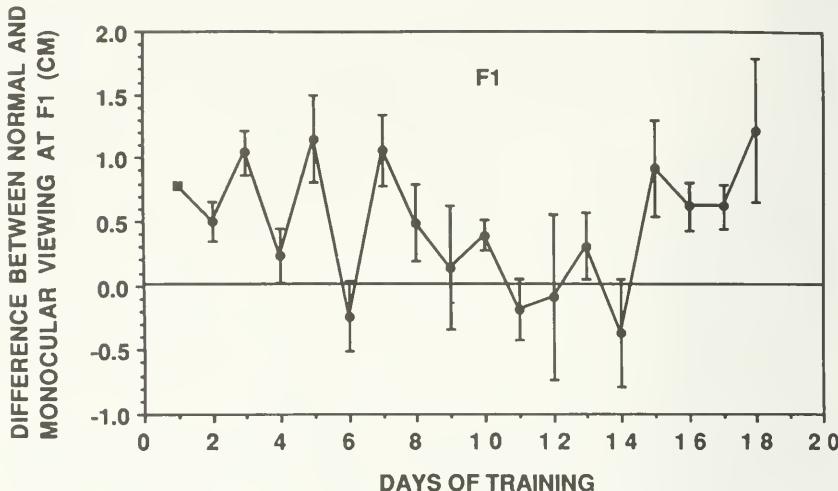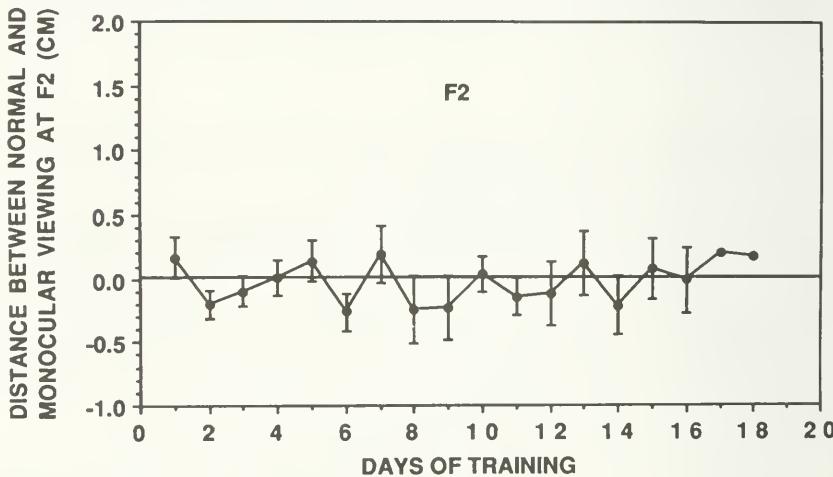
FIGURE 12. Effect of blocking binocular feedback on head fixation position for (A) F1 and (B) F2. Positive values indicate that the centre of the pupil was closer than normal to the seed. Negative values indicate that the eye was further away than normal. Bars show the standard error of the data.

FIGURE 13. Video frame image of a peck at a single grain of millet with prisms in front of both eyes (base out, 10 diopters). (A) Image at the last stationary fixation point F2. Note that the eye beak axis is

lined up with the centre of the grain. The distance from the centre of the pupil to the grain is 5.3cm. (B) Image of moving bird at the inflexion point in the peck movement in which the distance of the seed was underestimated by 5mm. Such short pecks were common in birds wearing prism spectacles. The fully opened eye of this particular frame also demonstrates the interference that was occasionally seen in the eye closure that normally accompanies the peck. In normal viewing, the eye always begins in close after F2 and is fully closed by the time the beak contacts the seed.

independent of the observer position. To this end both motion paral-
lax and stereopsis provide that extra dimension. Stereopsis relies on
convergence to facilitate fusion and provide the stimulus for horizon-
tal retinal disparity.

Within the frontal binocular field we have found that the pigeon
can use local stereopsis to estimate the relative position of objects in
its visual space (McFadden & Wild, 1986). We demonstrated that the
bird can discriminate the presence of depth between two arrays of
elements (black triangles of random size and orientation) only under
binocular viewing conditions. The binocular depth acuity for perceiv-
ing small displacements between two planes in space is best when a
distinct shape (such as a circle) is the emergent binocular stimulus.
Under these conditions, the stereoacuity is 1 minute of arc, a value
approximately matched to the photoreceptor density (McFadden,
1987). These measurements were done at a viewing distance of ap-
proximately 10cm. In previous work, we have been unable to obtain
binocular perception beyond 18-20cm when using stereoscopic stimuli
10mm in depth, despite extensive fading procedures. The mean num-
ber of trials for 4 birds in which no learning was evident was 4,680
(S.D. = 327). Just as the spatial visual acuity as measured with grat-
ings appears to be distance dependent (Bloch & Martinoya, 1982)
there also appears to be a limit to the best stereoscopic range within
the frontal field.

We have also measured distance and relative distance perception
in a task in which retinal image size was available as a major cue in
addition to enforced binocular viewing. This was achieved by the ap-
paratus shown in Figure 14. The bird was required to break a photo-
cell beam after which a brightly lit white disk (3.5cm in diameter)
was shown down a tunnel directly in front of the bird. The distance of
the target could be varied. Initially each bird was required to peck
the left key once if the disk was present and the right key if the disk
was withdrawn to 200cm (effectively absent). Correct responses were
rewarded with grain presented in the food hopper directly below the
tunnel entrance. The task was relatively difficult as the key response
had to be made after the head was withdrawn from the viewing tun-
nel and discrimination choice was based on the memory of the disk
position. Nevertheless, the task was learnt after 35 and 18 daily
sessions (96 trials/session) in two birds. Both birds were then tested
with the target presented at progressively greater distances (Figure
15A). After repeated testing, it was found that difficulty with the dis-
crimination occurred at a target distance of 18cm. At this distance
the target subtended 11°. When the viewing distance was 23cm the
presence of the disk could not be related to a correct key pecking
strategy. It is possible that the frontal field is perceptually limited in
terms of the distance at which objects can be discriminated. It is also
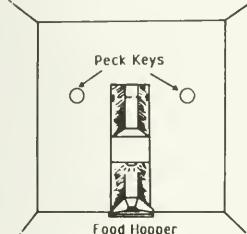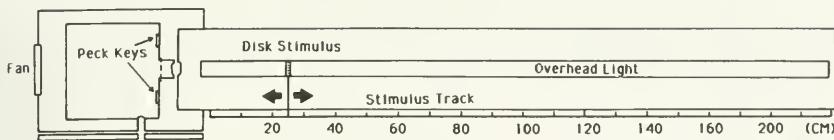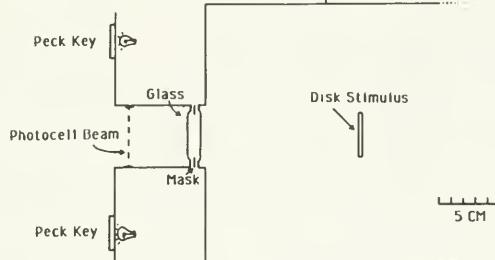
FIGURE 14. Apparatus used for measuring relative distance perception in the pigeon. (A) Top view in cross section showing the viewing tunnel attached to the operant chamber. The stimulus target was a white disk 3.5cm in diameter and could be moved on the stimulus track up and down the tunnel. (B) View of the front pecking wall as seen by the pigeon. (C) Enlarged view of part of A, showing the photocell beam and the tunnel behind it which the bird was trained to place its head in order to view the stimulus.

possible that accommodation is not adequate at distances of approximately 20cm in the frontal field.

It was also of interest to find that when both birds were tested at a viewing distance of 13cm for the smallest distinction that could be discriminated between two disk positions, the resultant mean relative distance threshold was 5.4cm (Figure 15B). This is equivalent to 4.4° in terms of the minimal discriminable difference in the size of the disk. Clearly, when forced to deduce the depth between two target positions based on comparing egocentric distance estimates, the resultant acuity is very much poorer than when access to binocular disparity is facilitated (retinal disparity was not available as the two target positions were not presented simultaneously). If the egocentric distance estimator in the frontal field was based on a vergence signal
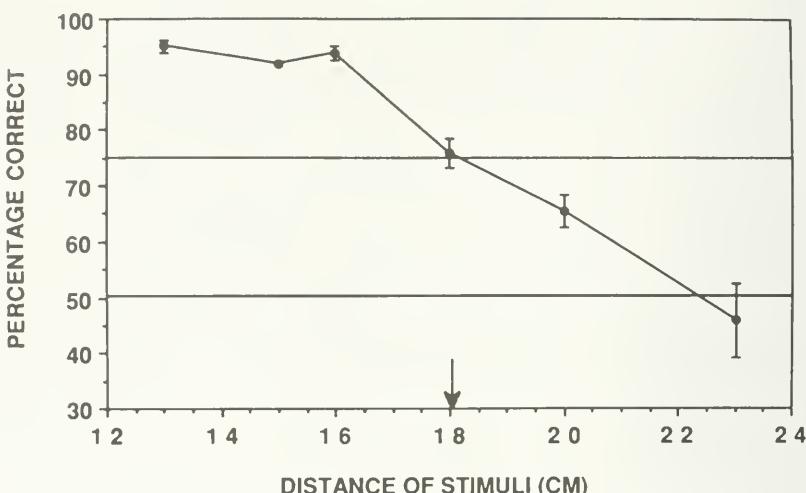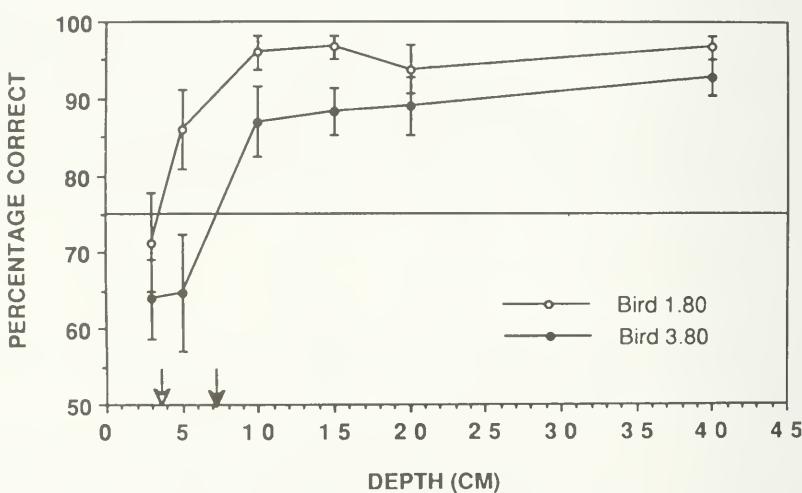
FIGURE 15. Mean performance of two birds trained in the apparatus shown in Figure 14. (A) Threshold for discriminating the absolute distance of the disk stimulus placed at various viewing distances from the eye. (B) Threshold for discriminating the relative distance between two disk positions, one of which was always placed at 13cm from the eye and the other placed at a further 3, 5, 10, 15, 20 or 40 cm. The threshold is taken halfway between perfect (100%) and chance (50%) performance. Standard error bars are shown.

as implied in the pecking studies, then this signal alone is inadequate for producing accurate relative distance perception. In contrast, retinal disparity, although alone it is not particularly useful for egocentric distance estimation, is a high resolution mediator for external depth perception.

GENERAL DISCUSSION

The finding that eye convergence is intimately linked to peck accuracy in a common reaching task in the pigeon and is binocularly sensitive at distances of approximately 13cm matches the optics of the pigeon's eye in which refractive state is relatively myopic in the frontal visual field and the depth of field may be limited. However, this vergence signal alone is relatively weak as an estimator of the relative positions of objects and is ineffective at distances greater than 20cm in the frontal field. Here we see that local stereopsis appears to be much more effective and raises the suggestion that this capacity which appears on the surface to be relatively independent of egocentric distance may be more useful for discriminating small distinctions in depth such as in objects viewed against a textured background. The resultant breaking of camouflage would be an effective means of pattern decoding in a stationary world.

Of course, there is little doubt that motion plays an prominent role in visual perception given the propensity for pigeon visual centres to contain motion cells (Donovan, 1978) and the spatial domain during flight. However, the need for stationary analysis of visual space should not be underestimated. In the pigeon, even during walking, head bobbing motions act to keep the spatial array constant (Friedman, 1975; Frost, 1978). So too, the converging eye movement that accompanies the peck response may result in maintaining the image of the grain on a constant area of the retina. As we have seen, the area dorsalis may well be such a candidate, with its high density resolution capacity.

Interaction between the vergence system mediating egocentric distance perception and stereopsis aiding in depth perception is likely to occur if depth constancy is an emergent feature of pigeon spatial vision. Perceptual constancies are more likely to be involved in the 'what' rather than the 'where' distinction proposed by Schneider (1969) and Ingle (1973). We are presently investigating this possibility, and such comparative studies may shed light on the evolution of visual pathways. Livingston & Hubel (1987) have suggested that depth perception is phylogenetically older than the capacity for colour and high resolution form perception developed in the parvocellular system of the primate geniculocortical visual system. The apparent

involvement of the supraoptic decussation in mediating distance perception in the pigeon visual system implies that such information is carried at least in part by the thalmofugal system rather than the more primitive and more prominent tectofugal pathway. It is perplexing to see that the same neural mechanisms may have convergently evolved in different species but by different pathways. The matching of the neural mechanisms may only serve to remind us that all species are constrained by similar physical properties of the spatial array.

ACKNOWLEDGEMENTS

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DEPTH/DISTANCE PERCEPTION IN GERBILS AND SPINY MICE: ECOLOGICAL CONSIDERATIONS

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ABSTRACT: Adult and young gerbils and spiny mice were tested for their ability to discriminate between a short and a long arm in a T-maze. Animals were given 20 training trials/day for 5 days. The gerbils' performance improved from about 45% correct responses on Day 1 to about 80% on Day 5; the performances of the spiny mice stayed at about 40-50% over the training period. There were no age differences. These findings complement those of an earlier study in which spiny mice did demonstrate depth perception on a visual cliff while the gerbils did not. Both sets of data are interpreted from an evolutionary perspective which relates depth perception ability to the organism's natural ecological niche: gerbils are burrowing animals and spiny mice are surface and rock dwellers.

A multifaceted comparative question we have been pursuing focuses on developmental aspects of various sensory systems in gerbils and spiny mice. That this is a useful question seems clear both from our own work and the work of others extending back many years (Honzik, 1936; Schiffman, 1970; Webster & Caccavale, 1966; Greenberg, 1986; Yahr, 1977). While these are closely related species (Ellerman, 1940/1966), there are many differences in their ecology. The spiny mouse (*Acomys cahirinus*) is primarily a rock-dwelling organism and does not burrow in regard to reproduction or food management, while the Mongolian gerbil (*Meriones unguiculatus*) is a burrowing animal.

Our first experiments (Greenberg, 1986) examined the depth perception abilities of these two species on a modified visual cliff. We concluded that both species demonstrated depth perception. The spiny mice showed this by increasing descent times as the platform height

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increased. Although descent times did not vary with platform height for the gerbils, their descent times were slower than those of the spiny mice at the shallow platform heights, suggesting that they were making cautious approaches to the platform drop-offs.

Subsequent replications of these studies (ms in preparation) have caused us to rethink our earlier conclusions. We now believe that while spiny mice do indeed display depth perception in these platform situations, gerbils do not. Their descent times simply do not vary significantly with platform height, a finding of our first study (Greenberg, 1986). However, the literature indicates that gerbils can perceive depth. Indeed, upon reading the published account of our research, a colleague sent a report of his research which shows good distance perception by gerbils when measured in a situation that requires the animal to jump horizontally from one ledge to another (Ellard, Goodale & Timney, 1984).

This caused us to reflect on the ecological differences between these species, as alluded to above. We reasoned that the platforms we had been using were more analogous to the natural environment of the spiny mouse than of the gerbil. Would the gerbil display depth/distance perception in a T-maze, in which the arms were analogous to the environment of a burrow?

METHOD

Animals. Twenty Mongolian gerbils (*Meriones unguiculatus*) and 28 spiny mice (*Acomys cahirinus*) were observed in this experiment. All animals were bred and raised in our laboratories, fed Purina lab chow ad libitum, and given free access to water (gerbils) or carrots (spiny mice). All animals were maintained in same sex pairs; the gerbils were housed in translucent shoe box cages (29.2 x 28.45 x 15.24 cm) on corn cob bedding and the spiny mice were housed in 10 gallon glass aquaria on a sand substrate containing a large rock. At the start of the experiment half of the gerbils were about 30 days of age and half were about 250 days of age; 8 of the spiny mice were about 60 days of age and 20 of the spiny mice were more than 1 year of age.

Apparatus. Animals were tested in a T-maze with a 51 cm main alley (including a 9 cm start box) and short (22 cm) and long (45 cm) choice alleys. The alleys were 10 cm wide and 14 cm high. Illumination was provided by a 52 watt white light suspended 70 cm above the choice point. The floor of the alleys were lined with clear plexiglass and the entire maze was enclosed with wire mesh to prevent animals from escaping. The entire apparatus was enclosed in a large cardboard box to minimize extra-maze cues.

Procedure. Ten days prior to the start of the experiment all animals were placed in individual cages and put on a 22 hour water deprivation schedule. Spiny mice were water deprived by removing carrots from their diets six days prior to the beginning of the experiment; they were given 2 hour free access to carrot pieces in their cages during this period. To assess the relative motivating properties of carrots and water for the spiny mice, 10 animals were maintained on an ad libitum water schedule for several weeks prior to the start of the experiment; ten days before testing began these animals were water deprived in the same manner as were the gerbils.

The ability of the animals to discriminate between the long and short arm of the maze was tested in five daily sessions of 20 discrimination trials. Correct choices were reinforced with saccharin sweetened water for the gerbils and unsweetened water and 5-10 mg carrot pieces for the spiny mice. For half of the animals the correct choice was the short arm and for half it was the long arm. The position of the correct choice was randomly assigned for each trial. When water was the reinforcement both arms contained drinking tubes, although only one provided water; when reinforcement was a carrot piece it was placed in a small food cup and a similar empty food cup was placed in the incorrect arm. Both maze arms, then, were visually identical.

All animals were allowed a single free exploration trial and a forced trial to the opposite arm prior to testing; both trials were reinforced. Trials consisted of placing the animal in the start box for 10 seconds after which time the door to this box was raised. The animals were then free to explore the maze. The arm the animal selected on each trial was recorded as a correct or incorrect response.

RESULTS

The mean correct responses made by the five separate groups over the five days of testing are shown in Table 1. This is illustrated in Figure 1. Both show that the gerbils improved their discrimination over the training period while the spiny mice did not. An ANOVA indicated no significant differences between the adult spiny mice reinforced with carrots and those reinforced with water ($F_{(1,18)} = 1.24$, $p < .28$) and so the results of those groups were pooled. A second ANOVA showed no significant age differences ($F_{(1,44)} = 0.44$); there was, however, a significant difference between the overall gerbil and spiny mouse performance ($F_{(1,44)} = 35.27$, $p < .001$). The Newman-Keuls Statistic revealed that Day 5 performance was significantly better than Day 1 performance for the young gerbils ($p < .01$) and the old gerbils ($p < .01$), but not for the spiny mice.

TABLE 1
Mean Correct Responses (20 Trials/Day)

		Day 1	Day 2	Day 3	Day 4	Day 5
Young gerbils	$\overline{\text{X}}$	9.1	10.7	13.0	14.6	16.5
	S.D.	1.4	5.1	5.3	4.9	7.4
Old gerbils	$\overline{\text{X}}$	9.9	11.0	11.6	13.5	14.1
	S.D.	2.8	3.8	1.6	13.7	7.7
Young spiny mice	$\overline{\text{X}}$	9.6	8.8	10.5	10.0	10.6
	S.D.	5.4	2.2	4.9	3.4	10.0
Old spiny mice	$\overline{\text{X}}$	8.7	10.7	10.7	9.5	9.6
	S.D.	8.7	6.0	1.6	7.2	6.9

DISCUSSION

These results indicate that gerbils can readily learn to discriminate depth/distance in a horizontal T-maze, while spiny mice apparently cannot, at least under the present conditions. However, the results of our earlier work (Greenberg, 1986) show that spiny mice can indeed make this discrimination when tested on a visual cliff, whereas gerbils cannot when tested this way. We believe that these differences in discriminating depth/distance reflect natural ecological adaptations made by these species. Gerbils are burrowing animals and our experiments show that they can discriminate depth/distance in the burrow-like arms of a maze: spiny mice are rock and vertical surface dwellers and they can discriminate depth/distance when tested on a cliff-like device.

Our interpretation of these data is consistent with the statement by Brown (1975) in a discussion of responsiveness to stimuli that are of biological significance to an organism, that "Evolutionary theory suggests that the nervous systems of animals have been specialized through natural selection for the performance of tasks relevant to the way of life of each species (p. 537)." This idea is related to the concept of "feature detectors" in sensory systems, initially described by Lettvin, Maturana, McCulloch and Pitts (1959) and now included in virtually all treatments of the neurophysiology of sensation and perception (Carlson, 1988). Indeed, there is even some evidence for the presence of depth detectors, neurons in the striate cortex which respond differentially to retinal disparity (Poggio & Poggio, 1984).

As structures, feature detectors are subject to evolutionary modification (Tierney, 1986). Such structural adaptations would seem to
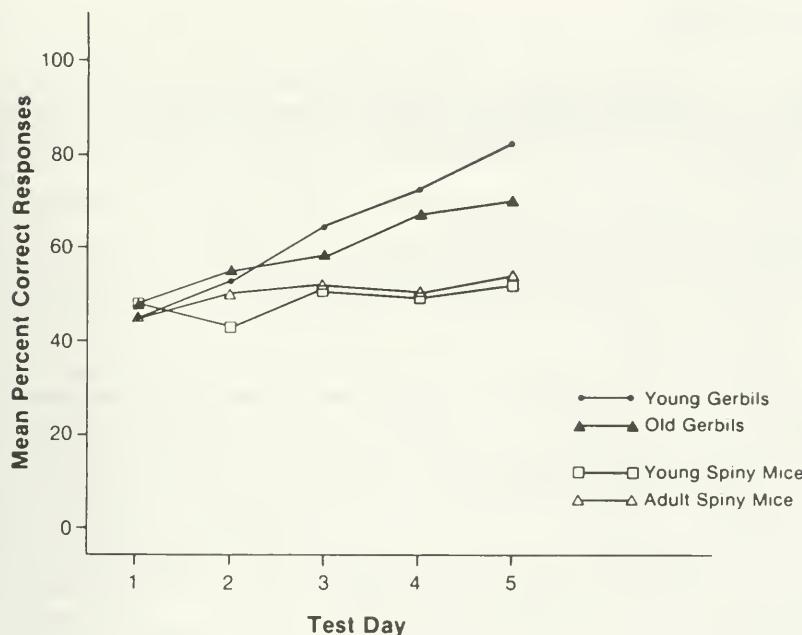
FIGURE 1. Mean percent correct responses.

be an an important basis for an organism's fit with its ecological niche as a recent analysis of the biophysics of burrowing behavior indicates (Reed, 1985). It is even possible to account for the ability of monkeys to identify conspecifics and their various facial expressions and characteristics by invoking the idea of inherited feature detectors (Perrett & Mistlin, 1990). What we are suggesting is that gerbils have evolved a visual system that functions more effectively in the horizontal dimension than it does in the vertical (a finding confirmed by Ellard, Goodale & Timney, 1984) while the visual system of the spiny mouse seems to function more effectively in the vertical dimension.

Another result of this experiment that warrants mention was the finding that the young gerbils outperformed the old gerbils on days 3 through 5. Although these differences were not significant, they are consistent with our earlier findings that young gerbils are superior to older ones in a simple visual discrimination task, and points to a developmental course of sensory efficiency (Greenberg, 1978; Greenberg & Dieffenbacher, 1976). We believe that vision is prepotent in this species early in its life and that other senses, such as touch, which is more involved in burrowing, become prepotent in adult animals. We are currently addressing this problem with the two species studied here.

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SERENDIPITY IN ANIMAL EXPERIMENTATION: EXAMPLES FROM DURATION SCALING IN RATS

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ABSTRACT: In the scaling experiment proper, 8 rats had to reproduce 10 randomly presented time intervals ranging from 1.3 to 20 s. The beginning of the reproduction was separated from the end of the standard by a 300 ms interruption of the sound indicating the durations. The rat determined the length of the reproduction by pressing a lever, thereby terminating the sound. The scaling model and the final result of the experiment are briefly described. However, before this final phase of the experiment, the rats had to learn to attend to the interruption. This was achieved in Phase 2 of the experiment by defining lever presses during presentation of the standard as incorrect behavior, which was penalized by withholding the reward and lengthening the actual standard duration by 4 s. Scrutiny of the Phase 2 data revealed two unexpected—serendipitous—findings. 1. The rats learned that they had committed an error (a faulty lever press during the standard) before they learned to suspend their lever presses; shorter response latencies for to-be-rewarded than for not-to-be-rewarded trials clearly indicated: "Knowing before doing." 2. A study of the distribution of first lever presses during the standard showed (a) that these lever presses were not evenly distributed (the hypothesis of a negative exponential distribution was rejected), and, more interestingly, (b) that 7 of the 8 rats hardly ever pressed the lever during a certain interval (for 5 of the rats the interval 3.3-4.5 s): "Temporal holes in the latency distributions." It pays to look not only at data when learning has been accomplished, but also during acquisition!

In a course I teach on "How to write papers for psychological journals," one of the rules presented in slogan form is "Don't write an autobiography." However, in order to describe serendipitous findings, as well as fortuitous events influencing the particular research I shall relate, namely duration scaling in rats, I have to break this rule.

The soil in which the two roots of the study grew was the interest of this Department of Psychology, under the direction of Gösta Ekman, in scaling in general, and in studies of time perception in particular. One of the still prevalent issues in direct scaling methods like magnitude estimation or ratio setting is to what extent the scales obtained mirror observers' number behavior rather than their sensations. I thought that the role played by number behavior in rats

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might be markedly smaller than in human observers, so that scaling in rats, if yielding results similar to those from psychology students, would support the validity of subjective scales obtained by direct methods. This idea was one of the two roots. The other was more concrete; at a talk at a congress in New York City, timing experiments with rats were described in which drug effects were studied. The outcome was interpreted as changes in activity levels and I thought that time or duration scales could give a more precise explanation. At that time I was working at Harvard University (with S. S. Stevens), where I had access to rats and instrumental conditioning equipment—a lucky coincidence.

I designed the experiment—I shall mention the details later—and got some help with the wiring of the rack. (This was before computers entered laboratories.) I knew very little about relays and the other devices used, and practically nothing about rats, except that they should be kept at 80% of their free feeding body weight when used in experiments. I got four rats and had learned the following when I left Harvard, long before the experiment was completed: 1. Female rats are not very good experimental animals (all four were females); 2. There are large individual differences; 3. Rats grow throughout their life. I had kept the poor animals at 80% of their weight when I took over and when I left Harvard they were emaciated; my departure probably saved them from death by starvation.

Back in Stockholm I made only two more mistakes: I underestimated the complexity of the apparatus required for my experiment and I tried to use mice (which were very cheap) as experimental animals. I had two apparatuses built that did not work reliably and the mice never seemed to learn, unlike the Harvard rats—a typical example of confounded variables. Were the mice or the apparatus designers to blame? Eventually the department hired a new and very capable engineer and I purchased male blackhooded rats from Denmark.

The scaling was to build on duration reproduction data. Ten different standard durations, ranging from 1.3 to 20 s in equal log steps, were presented at random as a distorted tone. After an interruption of 300 ms the sound resumed and was shut off by a lever press. The rats' (final) task was to press the lever when they experienced the duration of the sound after the interruption as equal to the standard duration presented in that trial (see below). Eight rats were included in the experiment.

THE PARALLEL-CLOCK MODEL

I had certain—not too explicit—ideas about how duration reproduction data could answer the questions posed: that a duration scale

of the level obtainable would give a better description of drug effects than the level of activity and that psychophysical scales are not an artefact of number behavior. Anyhow, in order to get an impression of the working of the experiment, to check on the suitability of the chosen stimuli as well as of the length of the interruption, I carried out a pilot study with human observers (i.e., students of psychology) as models for the rats. The outcome was unexpected. The data indicated that the observers did not keep the standard durations in memory. Instead they used two "sensory registers," one accumulating the total subjective duration (the subjective duration corresponding to sum of the standard and the reproduced durations) and the other the subjective duration corresponding to the reproduced duration. The two durations, standard and reproduced, are experienced as equally long when the difference between the contents of the two registers equals the contents of the second register (Eisler, 1975). Figure 1 should make this idea clear. This model of duration reproduction behavior (the "parallel-clock model") can be said, from the researcher's point of view, to be tantamount to halving the total duration. Regarding the reproduced duration as subjectively half the total duration makes it possible to construct a subjective ratio scale for duration.
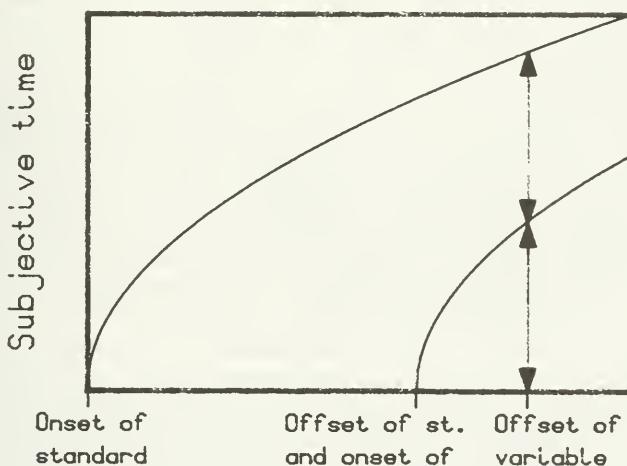
FIGURE 1. Duration reproduction according to the parallel-clock model. Subjective versus total physical duration (*left curve*) and versus reproduced duration (*right curve*). When the difference between these two subjective durations (*upper arrow*) equals the subjective reproduced duration (*lower arrow*), the observer reports equality between standard and reproduction by shutting off the sound.

Denoting subjective reproduced duration Ψ_r and subjective total duration Ψ_t, we obtain from the parallel-clock model

$$\Psi_r = (1/2)\,\Psi_t \tag{1}$$

Inserting Stevens' psychophysical power law

$$\Psi = (\Phi - \Phi_0)^\beta \tag{2}$$

where Ψ denotes subjective duration, Φ clock duration, and β and Φ_0 are constants, into Equation 1, we obtain

$$(\Phi_r - \Phi_0)^\beta = (1/2)(\Phi_s + \Phi_r - \Phi_0)^\beta \tag{3}$$

The subscript r refers to reproduction and s to standard; the total clock time, to which the total subjective duration Ψ_t corresponds, is $\Phi_s + \Phi_r$. By rearranging Equation 3 it can be seen that the reproduced duration is a linear function of the total duration. The parameters of the psychophysical function can be computed from the slope and intercept of a plot of reproduced against total duration. (For details, see Eisler, 1974, 1975.)

This surprising result, that a ratio scale of duration can be constructed from number-free duration reproduction data, should likewise permit the construction of a ratio scale for duration in rats, provided I could train them to reproduce durations.

In Figure 2 the outcomes of duration reproduction experiments with rats and humans can be compared. The figure shows plots for a session of a rat (left) and for a human observer (right). The lower plots are the raw data, reproduced duration plotted against total duration, the upper plots the psychophysical functions. To teach a rat to press the lever when it "experiences" the reproduced duration as equal to the standard, corresponding to the instruction to a human observer "press the button when the second sound has lasted as long as the first, " a "correct" region was defined. It was bounded for each standard by the shortest and longest reproduction made by any of the human observers for the standard in question. Responses within this region were reinforced. Naturally, not all ten durations could be presented from the start. The procedure had to proceed in steps, starting with two or three durations without overlap of the correct regions. Originally, I had thought I would have to narrow down this region around the rat's mean response, but this proved unnecessary; the rats seemed to make out the reproduction task quite well.

Communication with rats is even more difficult than with students of psychology. The experiment had to be carried out in three phases. The first was magazine training, the third the duration repro-
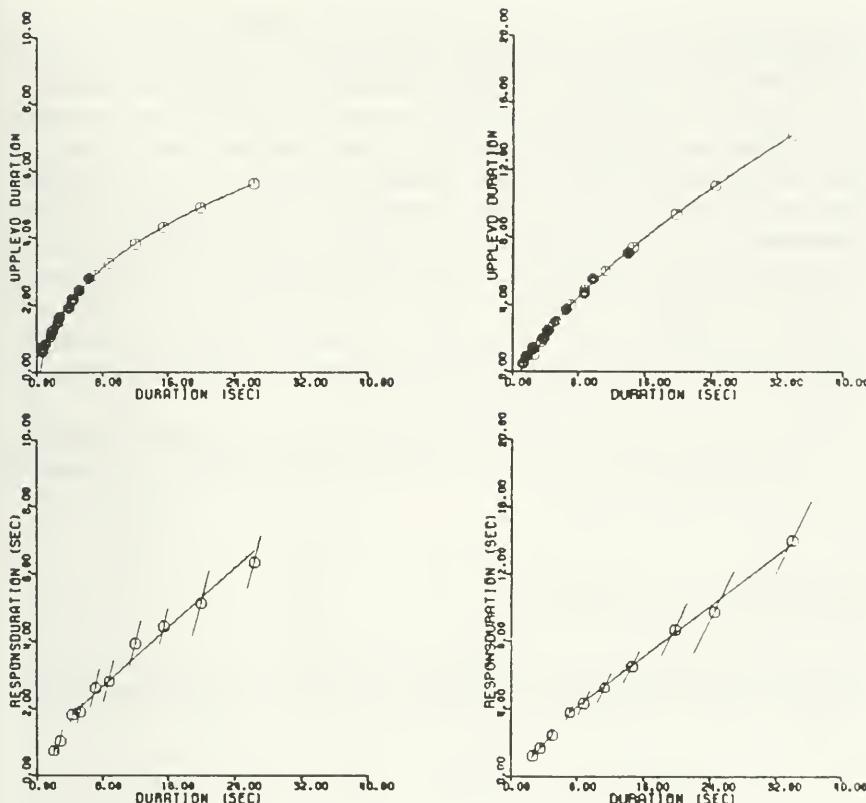
FIGURE 2. Duration reproductions from a rat (*left*) and a human observer (*right*). The *upper panels* describe the psychophysical power function, subjective versus physical duration. Black dots indicate goodness of fit. *Lower panels* show plots of reproduced duration Φ_r versus total duration Φ_t, together with the fitted straight lines. The slanted lines around the points are standard deviations.

duction experiment proper (the result of which is shown in Figure 2) and the second a training phase on which we shall dwell because it offers two examples of serendipitous findings in a narrower sense.

Experimental details can be found in Eisler (1984b, 1984c). Here I shall give only a brief description. We will remember that a trial consisted of an interrupted sound, with a standard duration before and a reproduced duration after the interruption. Trials were separated by a pause of 30 s and ended with access to sweetened milk as reinforcement, contingent upon "correct" behavior of the rat. What the rats had to learn in Phase 2 was to refrain from lever pressing during the standard duration, i.e., during the sound *before* the inter-

ruption, and to press the lever *after* the interruption. The aim of this procedure was to train the rats to attend to the interruption, which in Phase 3 was to be the demarcation between the offset of the standard and the onset of a duration to be terminated by a lever press when experienced as of the same length as the standard. Remember also that all the ten standards were randomly presented in the same session, a session comprising about 50-60 trials. A lever press during the standard gave rise, in addition to forfeiture of the reinforcement, to a prolongation of the sound by 4 s (the "punishment time"), in order to avoid superstitious chaining. Figure 3 shows two cycles (a cycle consists of a trial plus the long pause and possible reinforcement), a correct cycle in the upper panel and one with faulty lever presses in the lower.

The main interest was in the last phase, the duration reproduction phase, see Figure 2, but I was also curious about the course of acquisition during Phase 2.

KNOWING BEFORE DOING

A first observation was that the mean latencies between the end of the interruption and the lever press that terminated the sound (de-
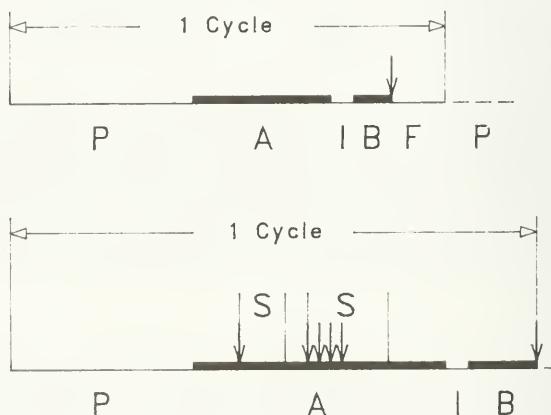
FIGURE 3. Cycle with reinforced (*upper panel*) and nonreinforced (*lower panel*) behavior patterns. The thick lines indicate the ongoing sound, vertical arrows donate lever presses, P the long pause, A the presented standard duration (in the lower panel lengthened by the punishment time S), I the interruption of the sound, B the latency between offset of the interruption and the following lever press, and F the feeding period. (From Eisler, 1987. Copyright 1987 by Elsevier Science Publishers. Reprinted by permission.)

noted by B in Figure 3) decreased with the number of sessions. The data treatment of this experiment was done while I was a Fellow-in-Residence at NIAS (Netherlands Institute for Advanced Study in the Humanities and Social Sciences) at Wassenaar. I happened to mention this finding to Eddy Roskam at the Katholieke Universiteit, Nijmegen, and he suggested separate looks at the latencies for trials with reinforced and not reinforced behavior, respectively. The result was astonishing: the latencies for correct trials (no lever press during the standard; reinforcement after the lever press) were short, almost from the beginning of Phase 2, whereas trials in which the rat had pressed the lever during the standard, so that no reinforcement was forthcoming, showed long (irregular) latencies throughout Phase 2 (See Figure 4). The decrease of the latencies during the course of Phase 2 was thus *not* a *general* decrease but reflected the decreasing frequency of trials with one or more incorrect lever presses, with their long latencies.

Note that the lever press terminating the sound occurred *before* the possible reinforcement, which thus could not have affected the preceding latency. Figure 4 also shows the acquisition curves, which demonstrate that the dissociation between short and long latencies had taken place before the rats' learning not to press the lever during the standard. The conclusion is that the rats knew of their faulty lever presses before they had learned to suppress them: "Knowing before doing" (Eisler, 1984b). This finding was not only unexpected, it was an unintended side effect of the main investigation and thus indeed serendipitous.

I sent a manuscript describing this finding to the *Journal of the Experimental Analysis of Behavior* where, after some linguistic changes (Skinnerian is not my psychological mother tongue), it was accepted, or so I thought. What happened, however, was that the journal acquired a new editor, who proposed a different explanation of the rats' behavior (that longer latencies were found for longer standard durations) and also pointed to a recent article by Shimp (1983) that did not seem to square with my findings. So I had to add an appendix to rule out the editor's hypothesis. Furthermore, I wrote another paper explaining Shimp's results (Eisler, 1984a): Serendipity on a higher level.

The hypothesis that longer durations entailed longer latencies could be refuted in the following way. As mentioned before, one lever press during the standard (A in the upper part of Figure 3) had the consequence of lengthening the sound before the interruption by 4 s. This made it possible to compare the latencies with and without an erroneous lever press for roughly the same durations A of the sound before the interruption. For instance, the standard duration 4.5 s approximates the 5.3 s which is composed of the standard 1.3 s and the
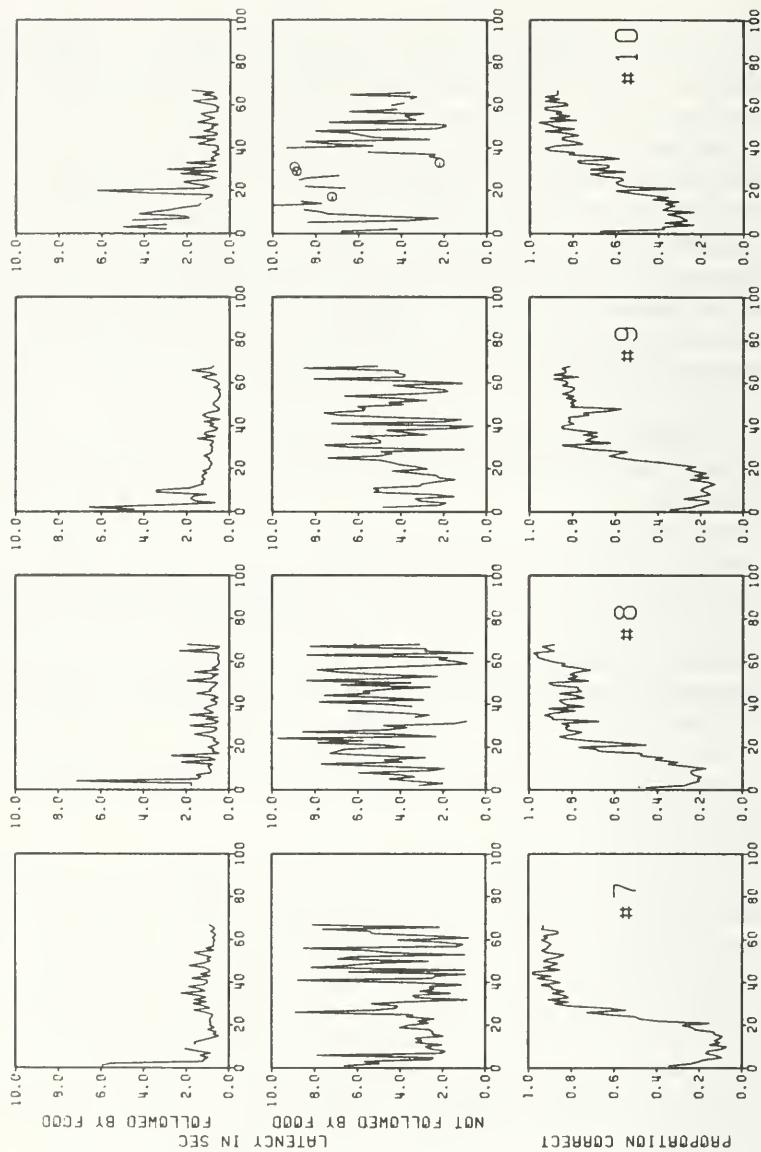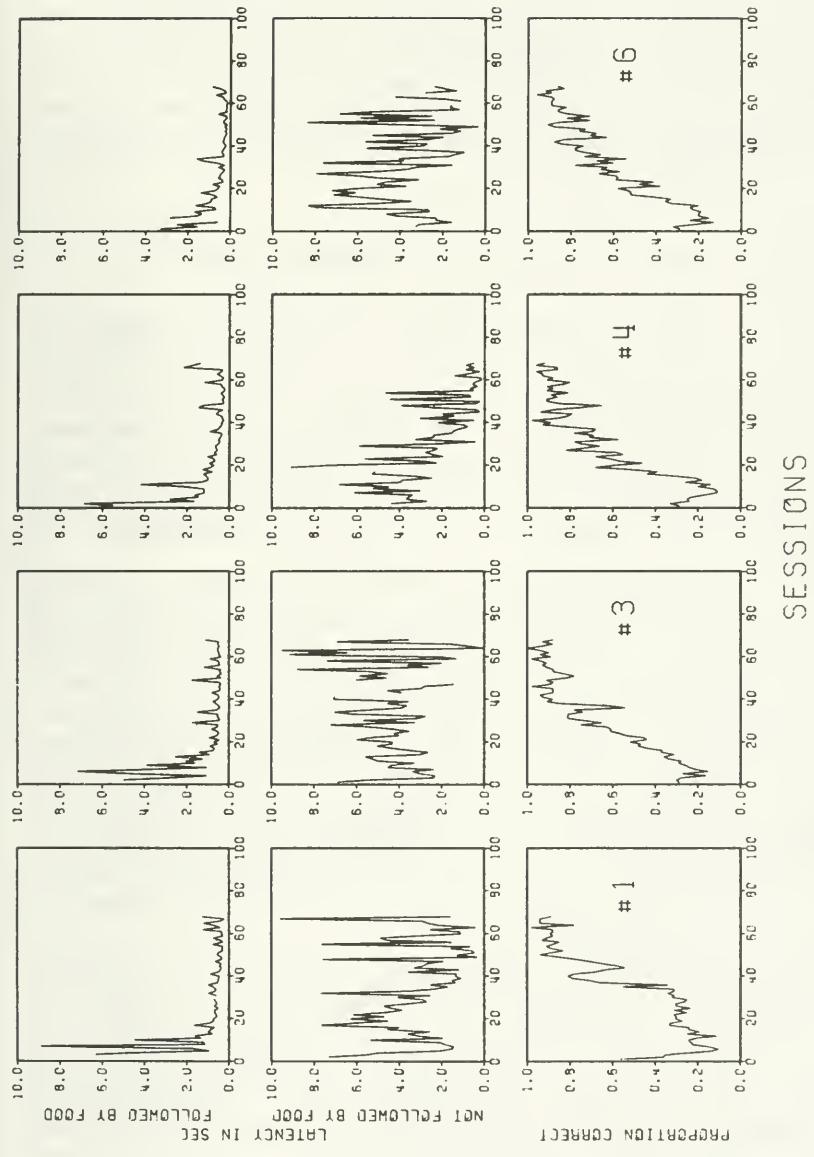
FIGURE 4. Acquisition curves (proportion of correct trials per session as a function of session number) and mean latencies with and without impending food as a function of session number for eight rats. Latencies exceeding 10 s are omitted. (From Eisler, 1984b. Copyright 1984 by the Society for the Experimental Analysis of Behavior, Inc. Reprinted by permission.)

punishment time of 4 s. Another example is the standard of 20 s and the combination of the standard of 14.8 s and the punishment time 4 s, yielding 18.8 s. An overall scrutiny of the pertinent latency data showed short latencies for trials with no lever press before the interruption, and long latencies for trials with one lever press, independent of the length of duration A.

TEMPORAL HOLES IN THE LATENCY DISTRIBUTIONS

Another problem is the distribution of faulty lever presses, in particular the latency from the start of the standard to the first lever press (before the interruption). For instance: does the rat's impatience grow with the length of the standard, thereby increasing the probability of such a faulty lever press? The equipment could not be used to determine the point in time of a lever press, only whether one (or more) had occurred in any one trial. Thus the distribution had to be inferred.

The longest standard was 20 s. This time interval was divided according to the differences between successive standard durations: 0-1.3 s, 1.3-1.8 s, . . . 14.8-20 s. The frequencies of trials with lever presses for any one such interval was determined as the difference between the frequency of the longer standard (say 1.8 s) and the next shorter one (1.3 s). A scrutiny of the data indicated that the distribution was irregular and that lever presses did not occur during certain of these intervals, namely those in which the frequency of trials with incorrect lever presses was about the same for two consecutive standard durations, e.g., for 1.3 and 1.8 s, so that the difference in frequencies for the interval in question (here the .5 s interval between 1.3 and 1.8 s) was close to zero.

The model describing *random* (first) lever presses is a negative exponential distribution with the cumulative distribution function $1 - e^{-\lambda t}$, where t is the observation period and λ the probability per time unit of the event, here a lever press. The parameter λ decreases with the number of sessions, because the animals learn to suppress lever pressing during the standard, but is assumed to be constant during a session. This model was rejected by a χ^2 test for all rats (fitting an average λ), which was to be expected from the study of the data mentioned above. In order to get a better description of the rats' behavior, the model was changed by replacing the clock intervals t by latent durations T, so that the negative exponential distribution holds. χ^2 was minimized by fitting 9 T values (for the intervals between successive standards) and 68 λ values for each rat. (Phase 2 comprised 68 sessions.) Figure 5 shows the latent duration T plotted against the clock durations t in log-log coordinates. What should be

Standard Duration
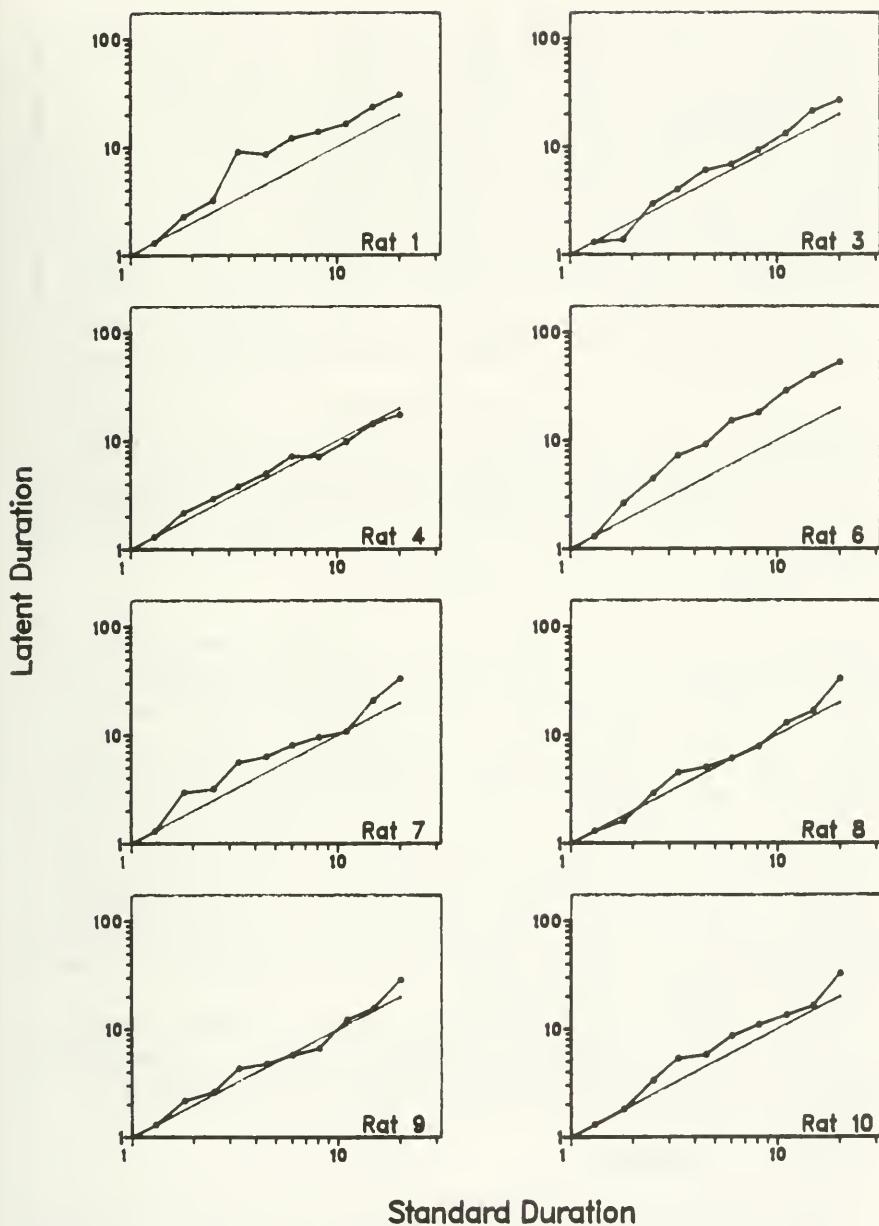
FIGURE 5. Latent durations T plotted against presented durations t for eight rats. The straight line indicates agreement between the two variables. Its slope should be compared with the slopes between adjacent points. (From Eisler, 1987. Copyright 1987 by Elsevier Science Publishers. Reprinted by permission.)
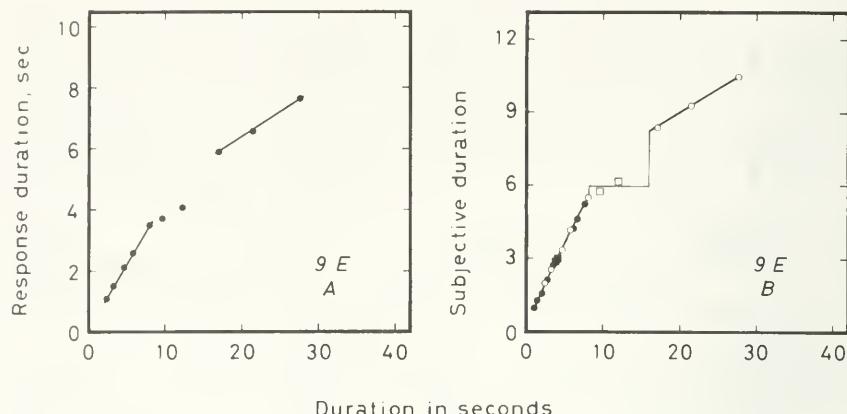
FIGURE 6. Duration reproduction for a human observer. Right panel: The psychophysical power function. Left panel: Reproduced duration vs. the sum of the standard and reproduced durations. (From Eisler, 1987. Data from Eisler, 1975. Copyright 1987 by Elsevier Science Publishers. Reprinted by permission.)

observed are the slopes. The lower the slope for a given interval, the shorter the latent duration compared to the clock duration. We see that for 7 of the 8 rats there are intervals with a slope close to zero. (For 5 rats this was the case for the interval 3.3-4.5 s.) In some sense these intervals do not exist for the rats; no lever presses took place. They are "temporal holes" in the latency distributions. This finding may be connected with the breaks and similar "holes" found in experiments with human observers, see Figure 6. An explanation could be a switch from one neural loop, corresponding to a certain duration, to the next (Thatcher, 1979; Thatcher & John, 1977). Details of this study can be found in Eisler (1987). Again, the finding of "temporal holes" is an instance of serendipity.

To conclude: it pays to keep your eyes open for unexpected findings in your experiments! Even if the problem focuses on steady-state behavior, a study of the acquisition phase may be worthwhile.

ACKNOWLEDGEMENT

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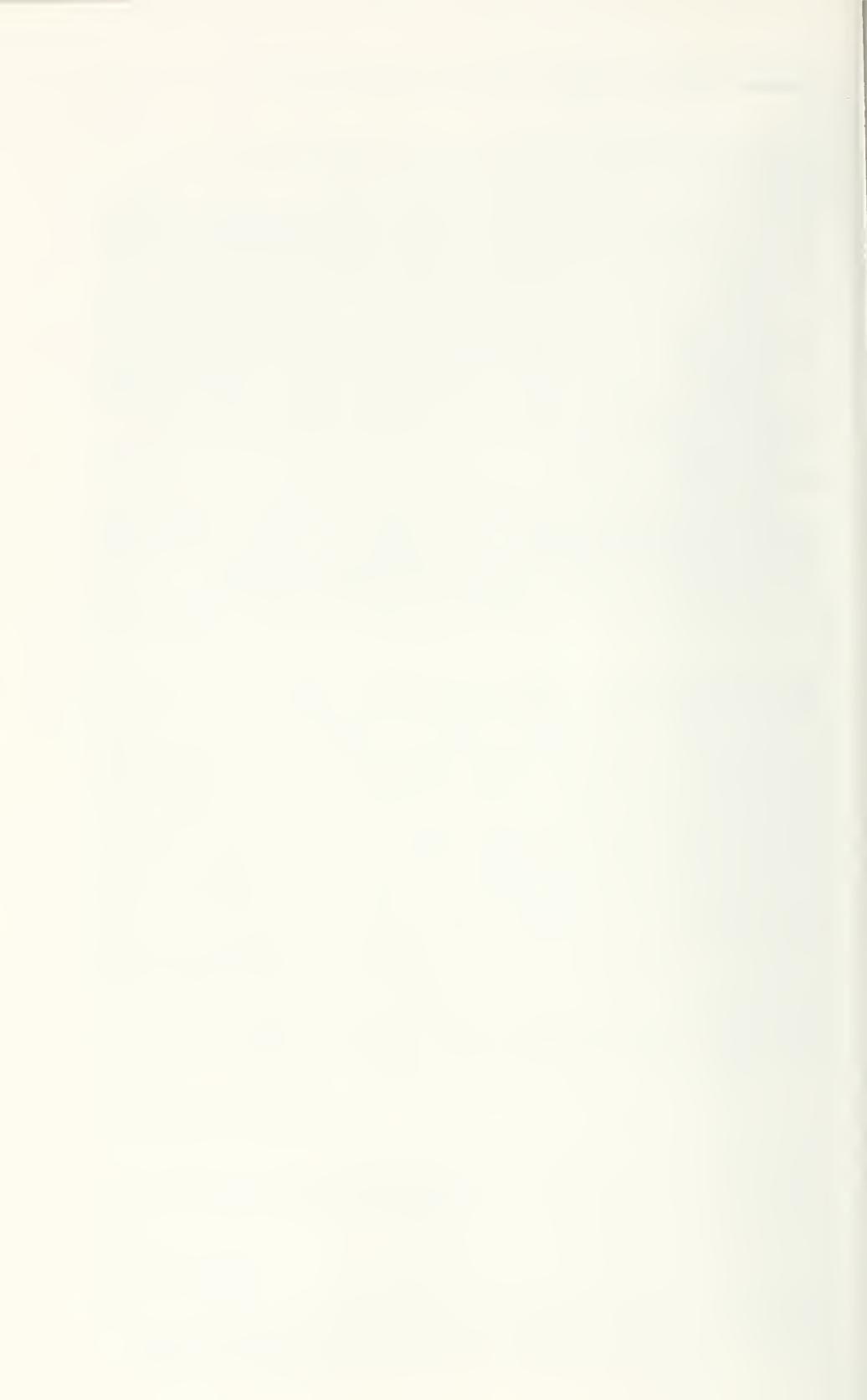
COMPARATIVE PSYCHOPHYSICS: SOME CONTEXTUAL EFFECTS IN BIRDS AND HUMANS

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ABSTRACT: Three different types of psychophysical context effects have been studied in comparative experiments with animals and humans. The main context variables investigated were: (1) range of the test series; (2) asymmetry of training to test stimuli (anchor effects); and (3) frequency distribution of the test stimuli. A two-stimulus, two response training procedure, followed by various generalization tests, was used. All subjects (19 chickens and 128 humans) were trained and tested with cubes of different sizes. The psychometric functions support the general assumption that perception in birds undergoes psychophysical context effects similar to that observed in humans. However, while all three variables affected the judgments of human subjects, the choices of chickens and human infants were not strongly affected by the frequency distribution of the test stimuli. These data suggest that two factors are responsible for the three contextual effects investigated: a basic perceptual factor invariant across species and age groups and a cognitive component.

Three main types of context variables have been studied systematically in psychophysics and frame-of-reference (FR) research: (1) the range of the test series (Witte, 1960; Parducci, 1965, 1974, 1983); (2) the relation of training to test stimuli; a special case of what Helson (1964) refers to as an "anchor" condition; (3) the frequency distribution of the test stimuli (Parducci, 1965, 1974, 1983). The effects of these three types of context variables on the psychometric functions will be described below.

The question as to whether and under which conditions animal perception can be experimentally demonstrated to be context-dependent, i.e., to be relative, has been discussed for almost 70 years. Ge-

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stalt theorists have interpreted transposition data as evidence that animals perceive relationships among stimuli (Köhler, 1918; Koffka, 1935; Wertheimer, 1959), while S-R theorists, following Spence (1937), have interpreted transposition data as resulting from summation of excitatory and inhibitory processes. Despite substantial research within the last few decades, this controversy has not yet been resolved (Reese, 1968).

Recently, the FR approach has been applied to the transposition problem (James, 1953) and to generalization studies employing asymmetrical testing procedures (Thomas, 1974; Sarris, Zoeke & Hofer, 1988; Zoeke, Sarris & Hofer, 1988). The theoretical and methodological advantages of an approach that combines quantitative modeling of relativity on the one hand, and the methodology of learning research on the other hand, promises solutions to basic problems of a comparative psychophysics including Köhler's (1918) earlier work on transposition, as well as Hollingworth's (1910) work on central tendency.

The present experiments provide a comparative investigation of context effects in animals and humans. How do birds respond to stimuli under the three context conditions described above? Are there differences between birds and humans? Is there any evidence for a species-specific distinction in how context variables affect performance?

According to Parducci's (1983) analyses, overt judgmental behavior in humans is to be conceived as a compromise between two different (covert) behavioral tendencies: (a) the tendency to subdivide the given range of test stimuli into equal sections (the range principle); and (b) the tendency to assign the same number of stimuli to each category used (the frequency principle). Anchor effects can be understood in terms of the range principle: Training stimuli and asymmetrical test series provide the experimental range which the subject has to subdivide into equal sections, an effect that becomes increasingly evident during continuous testing (see Johnson's 1949 a,b work on practice effects in asymmetrical testing with humans). Considering this analysis and the results of previous studies in animals (Zoeke, 1975; Sarris et al., 1988; Zoeke et al., 1988) we hypothesize that birds will subdivide a given range into equal subranges (showing range and anchor effects) but will fail on the more difficult task of assigning the same number of stimuli to each category (frequency effects).

EXPERIMENT 1—RANGE EFFECTS

The first study was directed to an examination of range effects in stimulus generalization of birds and humans. Figure 1 (left panel)
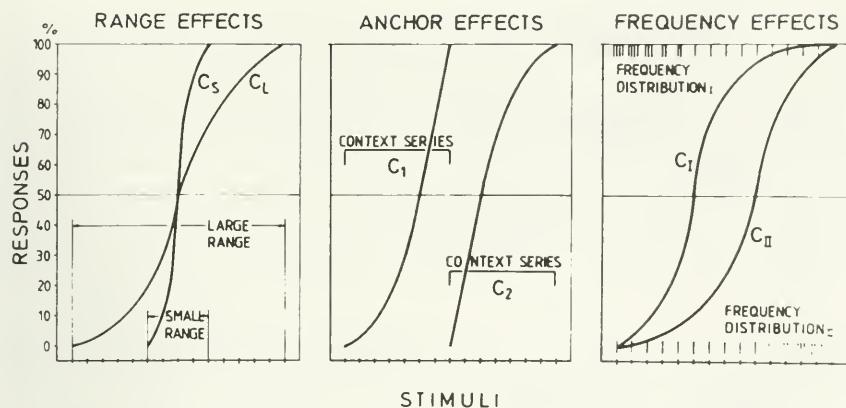
FIGURE 1. Predicted psychometric functions for three different types of psychophysical context effects. The left panel illustrates range effects: hypothetical response proportions are shown for a small (C_S) and a large (C_L) test range. The middle panel illustrates anchor effects: hypothetical response proportions for two asymmetrical test series (C_1, C_2) are shown. For C_1 the test stimuli are smaller than the training stimuli; for C_2 the test stimuli are larger. The right panel illustrates frequency effects: hypothetical psychometric functions are shown for a positively (C_I) and a negatively skewed (C_{II}) frequency distribution of test stimuli.

shows the predicted psychometric functions for a small (C_S) and a large (C_L) range condition.

METHOD

Animal Experiments

Subjects. Eight Hubbard chickens (*Gallus gallus domesticus*), six weeks old at the beginning of the experiment served as subjects. The chickens were kept as a flock in a scratching pen. Food was withheld for 18 hours prior to testing; water was continuously available.

Apparatus. Figure 2 (left panel) shows the computer-controlled apparatus permitting successive presentation of three-dimensional objects. The stimuli were presented in front of a 60x60x60 cm wall on which two pecking keys and two food magazines were fastened, one to the left and the other to the right of the area in which the stimuli could be shown. The objects were fixed underneath the test box, each on an individual plate, located on a rotatable wheel (diameter: 165 cm). A motor turned the wheel to the appropriate position, then the
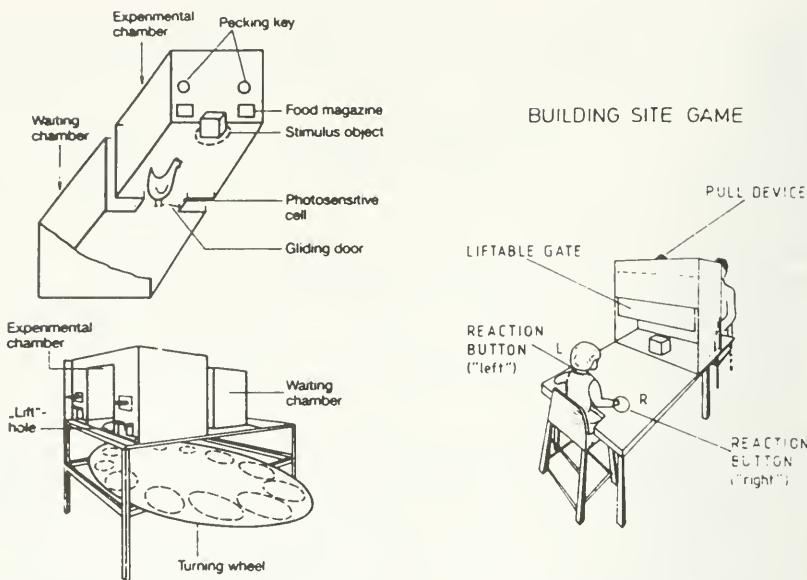
FIGURE 2. Schematic view of both apparatuses used in these experiments. The left panel is a schematic diagram of the animal apparatus. Top: test and waiting chamber with the subject, the cube, two pecking keys, and two food magazines. Bottom: automatic stimulus presentation device with an object attached to a plate located on a rotatable wheel. A motor turns the wheel to a predetermined position, then the plate with the chosen object is lifted hydraulically into the test box. The right panel is a schematic diagram of the apparatus used for the human subjects.

plate with the object to be presented was lifted to the floor of the test box (for additional details see Zoeke et al., 1988).

Stimulus material.   The stimuli were orange cubes differing in volume. All subjects were trained with the same pair of training stimuli (TS), a 128 ccm and a 512 ccm cube, but tested with two different sets of stimuli. The test stimuli were equally spaced on a log scale with the geometric mean of the two training stimuli defining the midpoint of both series. The small-range test series, C_S, consisted of five stimuli with the training stimuli, 128 and 512 ccm cubes, defining the upper and lower limits of the set. The stimuli were 128, 181, 256, 362, and 512 ccm cubes. The large-range test series, C_L, consisted of nine stimuli, cubes of 64, 90.5, 128, 181, 256, 362, 512, 724, and 1024 ccm.

Procedure.   After training to peck the key that was illuminated in order to obtain food, the subjects learned to peck key 1 if TS 1, the

128 ccm cube, was presented, and to peck key 2 if TS 2, the 512 ccm cube, was shown. Key positions were counterbalanced across subjects. Daily training sessions consisted of 30 trials. In this and all subsequent experiments, the training stimuli were presented in random order with the restriction that each stimulus was presented with equal frequency. Pecks at the correct key were reinforced by access to the food magazine for 3 sec. Darkness immediately followed an incorrect key choice and the same stimulus was presented immediately thereafter.

After reaching the learning criterion (95% correct choices for three successive training sessions) the eight subjects were assigned randomly to the two test conditions (C_S, C_L). Each series of five or nine stimuli was presented 10 times during 10 test sessions. All choices were reinforced.

Human Experiments

Subjects. Eight young adults (about 20 years old), non-paid volunteers from an introductory psychology class, served as subjects.

Apparatus. Figure 2 (right panel) shows the apparatus used for the three experiments reported here. The subjects were seated at a distance of 80 cm in front of a gate that could be lifted. Behind this gate the test stimuli, orange cubes differing in volume, were presented in random order. One of two blue buttons at the right or left hand of the subject had to be pushed down in order to indicate whether the cube was "small" or "large."

Stimulus material. The stimuli were the same as those used for animal experiments.

Procedure. The subjects were told to press one of the reaction buttons if TS 1, the 128ccm cube, was presented and to press the other reaction button if TS 2, the 512 ccm cube, was presented. All correct responses were verbally reinforced with errors corrected immediately. After reaching the learning criterion (20 consecutive correct responses) the experimenter instructed the subjects that they now had to continue without further interactions with the experimenter. The eight subjects were assigned randomly to the two test conditions (C_S, C_L). Each series was presented 10 times in a row. The test was completed within a single session.

RESULTS AND DISCUSSION

Figure 3 (top row) shows the results of the generalization tests for birds (left) as well as for humans (right). Each data point represents the combined average of 10 choices for each subject. The psycho-

metric functions are very similar for the humans and the chickens. For both groups the functions obtained with the smaller range, C_S, are steeper than those obtained with the larger range, C_L. This is confirmed by the finding that the proportions of "large" judgments for the two test series (C_S, C_L) are significantly different for the 181 and 362 ccm cubes (for chickens: chi-square $(1, 79) = 5.64$, $p<.02$ for the 181 ccm cube, and chi-square $(1, 79) = 4.51$, $p<.05$ for the 362 ccm cube; for humans: chi-square $(1, 79) = 5.72$, $p<.02$ and chi-square $(1, 79) = 4.32$, $p<.05$). The differences in proportions of "large" judgments for the two groups are insignificant ($p<.05$) for the 128, 256 and 512 cubes as expected.

The range principle predicts that the psychometric function should be steeper under C_S than under C_L since it is hypothesized that the test stimulus range is divided into equal parts. The data for both the human and animal subjects confirm this hypothesis.

EXPERIMENT 2—ANCHOR EFFECTS

The second study was directed towards an examination of anchor effects in generalization testing with birds and humans. Figure 1 (middle panel) shows the predicted psychometric functions for two asymmetrical test series.

METHOD

Animal Experiments

Subjects.   —Four Hubbard chickens (*Gallus gallus domesticus*), approximately seven weeks old at the beginning of the experiment, served as subjects. Housing conditions were the same as described in Experiment 1.

Apparatus.   —The apparatus was the same as in Experiment 1.

Stimulus material.   —The stimuli were orange cubes differing in volume in equal logarithmic steps. All subjects were trained with the same pair of TS, a 215 ccm and a 608 ccm cube, but tested with two different test series. The test stimuli were seven cubes, with volumes equally spaced on a log scale. The geometric mean of the training stimuli defined the largest test stimulus of the small contextual series, C_1, and the smallest test stimulus of the large contextual test series, C_2. For C_1 the test stimuli were cubes of 45, 64, 90.5, 128, 181, 256, and 362 ccm; for C_2 the test stimuli were cubes of 362, 512, 724, 1024, 1448, 2048, and 2896 ccm.

Procedure. —The procedure was similar to that described in Experiment 1. After key training subjects were trained to peck key 1 if TS 1, the 215 ccm cube was presented, and to peck key 2 if TS 2, the 608 ccm cube was presented. Daily training sessions consisted of 50 trials. After reaching the learning criterion (95% correct responses for three successive training sessions) the four subjects were assigned randomly to each text condition (C_1, C_2). Each series of seven stimuli was presented six times daily during sex test days.

Human Experiments

Subjects. —Twenty young adults (about 18 years old) served as subjects. Subjects were non-paid volunteers from a high school.

Apparatus. —The apparatus was the same as for Experiment 1.

Stimulus material. —The stimuli were again orange cubes differing in volume. All subjects were trained with the same pair of training stimuli, a 32 ccm and a 256 ccm cube but tested with two different test series (C_1, C_2). The test stimuli were equally spaced on a log scale. For the context series, C_1, five of eight cubes were smaller than TS 1; for context series, C_2, five stimuli were larger than TS 2. Both test series included two stimuli of the same volume (64 ccm, 128 ccm), the largest and the smallest under C_1 and C_2 respectively. For C_1 the test stimuli were cubes of 1, 2, 4, 16, 32, 64 and 128 ccm. For C_2 the test stimuli were cubes of 64, 128, 256, 512, 1024, 2048, 4096 and 8192 ccm.

Procedure. —The procedure was similar to that described in Experiment 1. After reaching the learning criterion (20 correct responses in a row), the 20 subjects were assigned randomly to the two context conditions (C_1, C_2). Both series were presented six times consecutively within a single session.

RESULTS AND DISCUSSION

Figure 3 (middle row) shows the results of the asymmetrical generalization test (C_1, C_2) for birds (left panel) and humans (right panel). Each data point represents the averaged choices of the last two of the six test sessions. The final test sessions were used for analysis since anchor effects become most evident as testing proceeds (see Zoeke *et al.*, 1988). Note, especially, that for the two test conditions, C_1 and C_2, the differences in the percent of large judgments for the two stimuli of the same volume (the 362 ccm cube for the birds, and the 128 ccm cube for the humans) are highly significant ($p < .001$). For the birds chi-square $(1, 47) = 37$; for the humans chi-square $(1, 39) = 32$.

The results of experiment 2 support the assumption that judg-
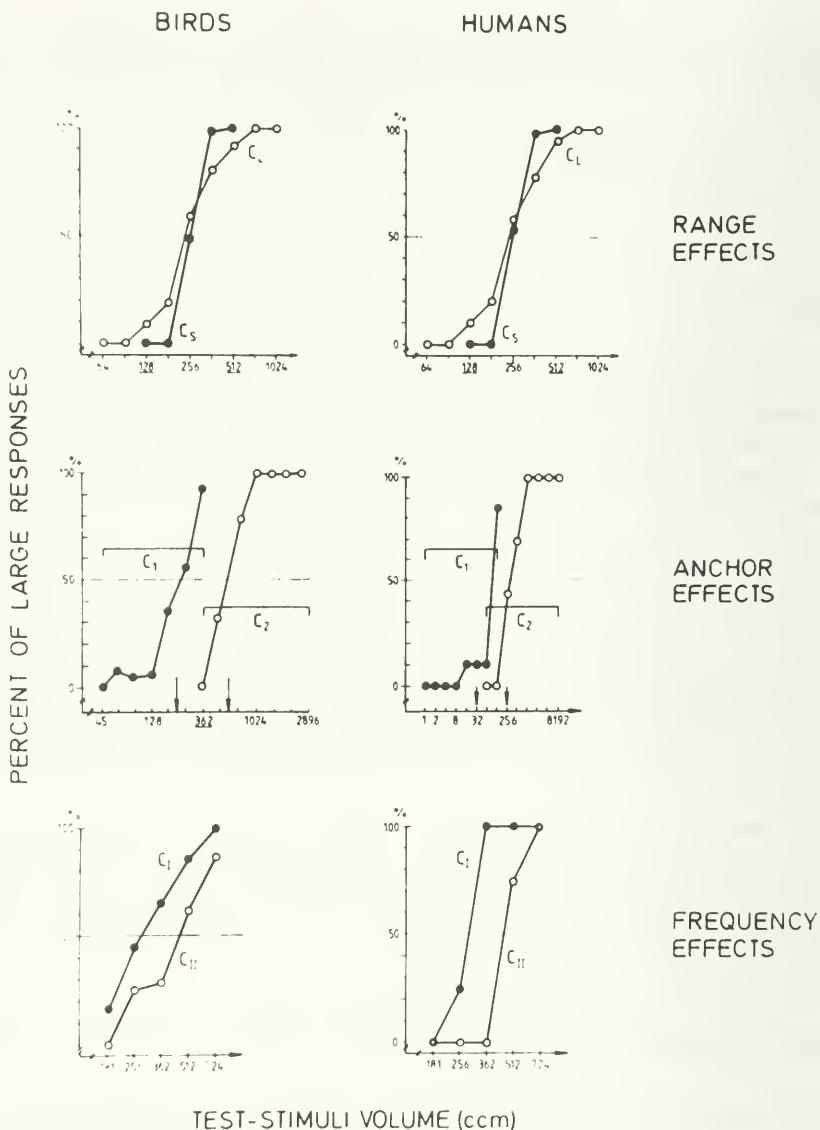
FIGURE 3. Empirical psychometric functions for birds (left) and humans (right). Top Row: Range effects—response rates for a small (C_S) and a large (C_L) test range. Middle Row: Anchor effects—response rates for two asymmetrical test series (C_1, C_2) either smaller or larger than the training stimuli. Bottom Row: Frequency effects—psychometric functions for a positively (C_I) and a negatively skewed (C_{II}) frequency distribution of test stimuli.

ments of birds are relational in character. With continued testing, the birds and the human subjects showed similar behavior when presented with the asymmetrical testing procedure.

EXPERIMENT 3—FREQUENCY EFFECTS

The third study was directed to an examination of frequency effects in stimulus generalization with birds and humans. Figure 1 (right panel) shows the corresponding prediction for two test series (C_I, C_{II}) differing in the frequency distribution of stimuli.

METHOD

Animal Experiments

Subjects.   Seven White Leghorn chickens (*Gallus gallus domesticus*), six weeks old at the beginning of the training, served as subjects. Housing conditions were the same as described in Experiment 1.

Apparatus.   The same apparatus was used as in Experiment 1.

Stimulus material.   All subjects were trained with the same pair of TS, a 181 ccm and a 724 ccm orange cube, and tested with five cubes of 181, 256, 362, 512 and 724 ccm. The frequency distributions of test stimuli were 7, 3, 3, 1, 1 (C_I, positively skewed) and 1, 1, 3, 3, 7 respectively (C_{II}, negatively skewed). A test series consisted of 15 trials with the frequency with which each of the five stimuli were presented defined above. The presentation order was random with these restrictions.

Procedure.   The training procedure was the same as described in Experiment 1 with the exception that the training sessions consisted of 50 trials. During training the presentation probabilities for the two stimuli were equal. After reaching criterion (95% correct responses) the proportion of trials on which food was delivered following a correct response was reduced from every trial to an average of one in 15. This was done to prepare for testing.

For testing, the birds were then assigned randomly to one of the two frequency conditions (C_I, C_{II}). A test session consisted of two presentations of the 15 trial test series. Food was delivered only once during this series with the trial on which this occurred randomly determined. Between each test series the two training stimuli were presented ten times each in a random sequence with reinforcement following each correct response. After two test days in which one of the

frequency conditions was in effect (four series presentations each) there was a shift to the second frequency condition (C_I to C_{II}, or C_{II} to C_I, respectively).

Human Experiments

Subjects. In addition to a group of 20 young adults comparable to those who served as subjects in the previous experiments, there were four younger age groups: 20 infants (20 to 26 months old), 20 kindergarten children (about 4 years old), 20 school beginners (about 8 years old) and 20 school children (about 12 years old). Gender was balanced in all age groups. Subjects were from four nursery schools, three kindergartens and two public schools.

Apparatus. The apparatus was the same as in Experiments 1 and 2.

Stimulus material. The stimuli and frequency distribution of these stimuli were the same as those described for the animal experiment.

Procedure. The training procedure was the same as described in Experiments 1 and 2. After reaching the learning criterion (20 correct responses in a row) the subjects of all age groups were assigned randomly to one of the two frequency conditions (C_I, C_{II}). The test was the same as that described for the birds except that individuals were tested under one condition and testing was done in a single session.

RESULTS AND DISCUSSION

Figure 3 (bottom row) shows the results of the generalization tests under the two frequency conditions (C_I, C_{II}) for birds (left) and humans (right). In this figure only the data obtained from the young adults are presented. Each data point represents the choices averaged over all subjects for the two series. For the young adults, the frequency effects are as expected (Parducci, 1965). The subjects adjusted the proportion of their responses according to the presentation probabilities. The response "large" is used more frequently for small cubes when the small cubes occur with greater frequency (e.g., compare the percent of "large" judgments for the 362 cm cube). Single case analysis showed significant effects of the frequency manipulation for all subjects.

The data obtained from the birds are quite different. The frequency manipulation had little effect. For data averaged across subjects, all differences were insignificant ($p > 0.05$). However, examination of individual test data showed significant differences as a function of frequency distribution for two of the seven birds: For one

bird chi-square $(1, 119) = 13.33$, $p<.003$; for the second bird, chi-square $(1, 119) = 7.67$, $p<.005$. Figure 4 shows the results of these two birds.

The data for the human subjects of the five age groups tested under the two frequency conditions are shown in Figure 5. From this figure it can be seen that the frequency manipulation affects performance to a greater extent as age progresses. The infants showed almost no effect of the frequency manipulation. The intermediate age groups showed intermediate effects. The frequency manipulation affected the choices of the high school children almost as strongly as it did the choices of the adults. Examination of the data of the individual subjects shows an effect of the frequency distribution of the performance of 2 of the 20 infants, 11 of the 20 kindergarten children, 14 or 20 school beginners, 15 of the 20 high school children, and all 20 adults.

These results suggest the *frequency* effects are species-specific as well as age-specific.

GENERAL DISCUSSION

All together the results of these three experiments corroborate the basic assumption of FR models in psychophysics that judgments are relational in character. This holds true for birds, as well as, for humans.
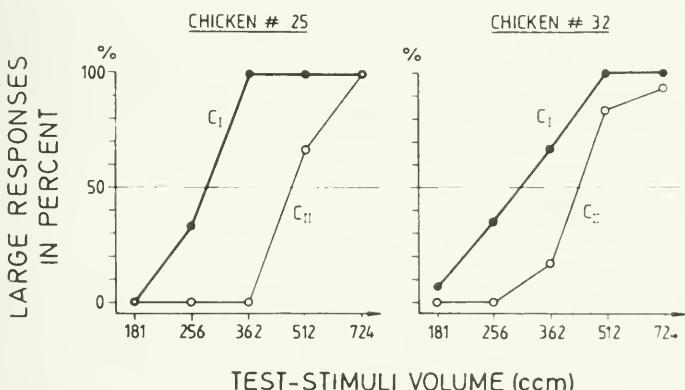
FIGURE 4. Empirical psychometric functions showing frequency effects in two birds for a positively (C_I) and a negatively skewed (C_{II}) frequency distribution of test stimuli.
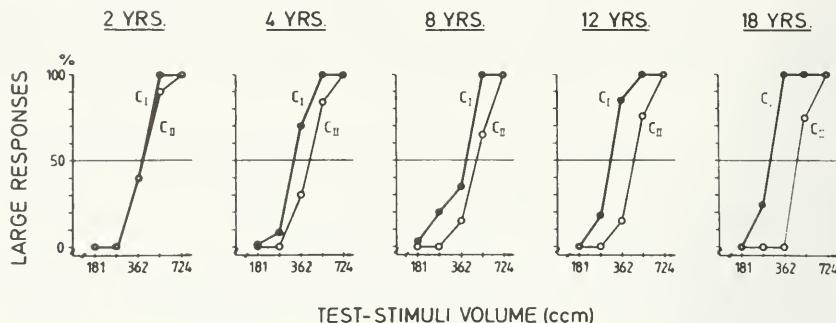
FIGURE 5. Empirical psychometric functions showing the effects of the frequency manipulation for different age groups for a positively (C_I) and a negatively skewed (C_{II}) frequency distribution of test stimuli.

While the responses of both species were strongly affected by range and anchor variables, the frequency distribution did not strongly affect the choices of birds and young children. Wedell and Parducci (1985) point out that under frequency conditions subjects have to pay attention to the size of the test stimuli as well as to their frequency distribution. Assigning the same number of stimuli to each category requires that relevant context information be retrieved from memory (i.e., the subject must remember both the range and the frequency distribution of the stimuli). Even adult humans underestimate the frequencies of those stimuli that occur more often (Wedell & Parducci, 1985).

Further studies have to be done to test the assumption that the cognitive demands of the frequency manipulation are greater than those involving either the range or asymmetry of the test stimuli. For instance, the differences among animals, young children and adults may be less pronounced when fewer stimuli are presented.

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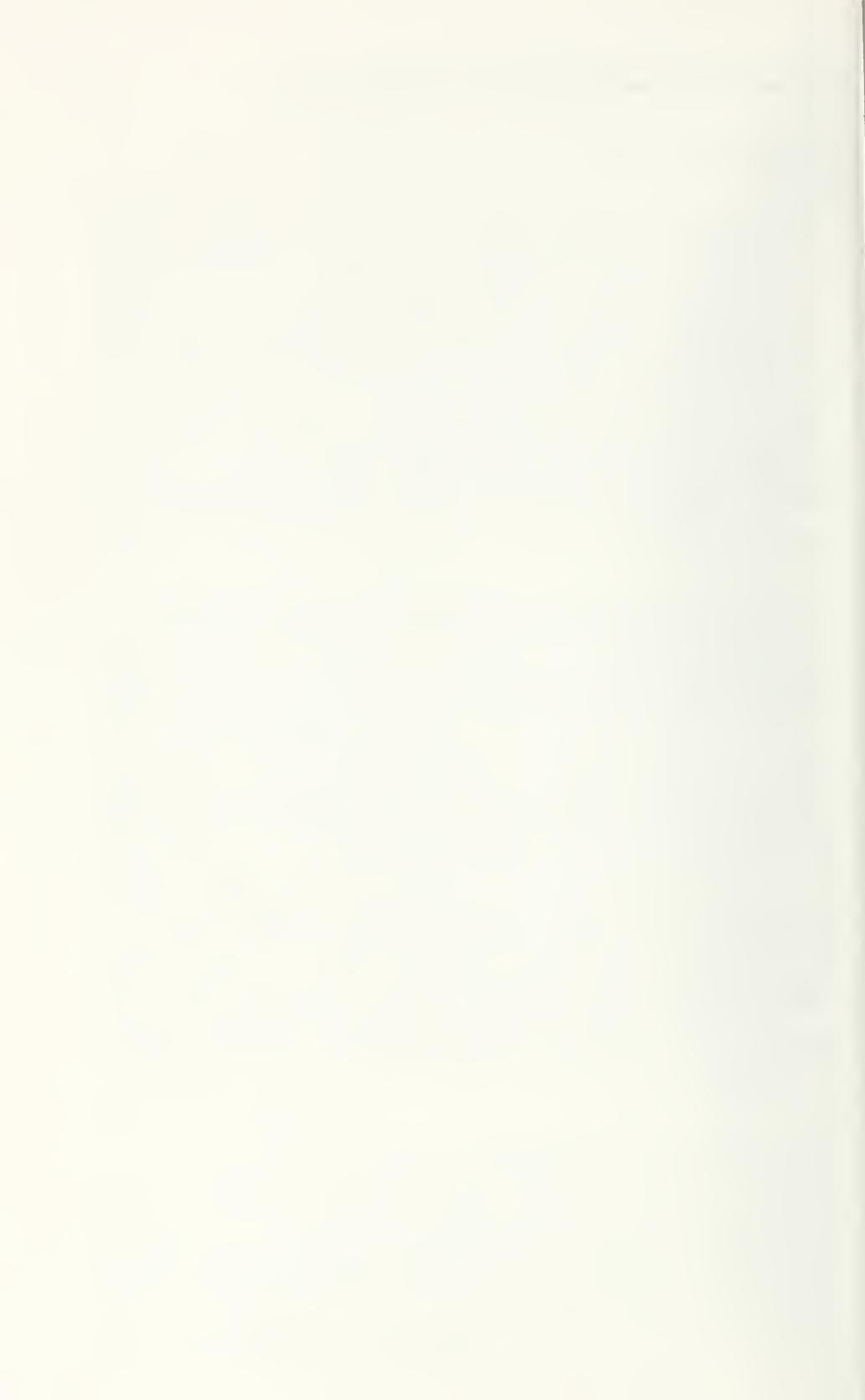
EFFECTS OF STIMULUS COMPLEXITY ON IDENTIFICATION AND CATEGORIZATION

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Eric G. Heinemann
Brooklyn College

ABSTRACT: Data are presented showing that humans and non-humans are severely limited in their ability to identify stimuli that vary along a single dimension. Increasing the dimensionality of spatially undifferentiated stimuli improves performance. However, this improvement is trivial compared to that observed when spatially complex stimuli, such as pictures, are presented for identification. The theoretical account of memory and decision processes presented here suggests that, while the number of items that can be held in working memory varies among species, the number of items that can be identified depends more upon the characteristics of the stimuli than upon the organism making the identification.

There are remarkable similarities in the way human and non-human animals discriminate among, identify, and categorize sources of stimulation. For example, both humans and other animals are severely limited in their ability to identify stimuli that vary along a single dimension, such as the intensity of a light, yet they easily identify vast numbers of complex stimuli, such as pictures. We shall provide a theoretical account of identification performance based on the premise that the behavioral similarities described reflect similarities in the underlying decision processes.

Our account of identification performance assumes that a stimulus is identified only when it roughly matches a record of a past event held in *working memory*. Differences in the number of items that can be identified correctly depend upon the capacity of this working memory and the type of stimuli to be identified. We will present preliminary data that suggest that three species—pigeons, monkeys and humans—differ in the number of records of past events that can be held in working memory. We will also suggest that increases in stimulus complexity activate a process of retrieving repeated samples

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of information from long-term memory which, in turn, results in an increase in the number of stimuli that can be identified.

## MEMORY SAMPLING MODEL OF DECISION MAKING

Although our model for the learning and decision process was originally developed to account for the behavior of pigeons, it also applies in some interesting ways to identification and categorization behavior in other species. The structure of the model and its parameters are described briefly here. For more detailed treatments see Heinemann, (1983a,b), Chase, (1983), Heinemann and Chase, (1990), Chase and Heinemann, (1991, in press).

An experiment of Heinemann, Avin, Sullivan and Chase (1969) illustrates the type of experiment for which our model was first developed. Pigeons were trained to identify, by pecks on the appropriate response key, two sounds that differed only in intensity. They were rewarded with food for making one response, R_1, when presented with the softer sound, and an alternative response, R_2, when presented with the louder sound. For one group the two sounds differed by 2.3 dB, for a second by 7 dB, and for a third by 29 dB.

The course of acquisition was typical of that observed in many experiments of this sort. At the beginning of training, there was a period during which there was no evidence of discrimination, the *pre-solution period* (PSP). The length of this PSP (number of trials) was inversely related to the difference between the two sound intensities. The PSP was followed by a gradual improvement in the accuracy of the discrimination. After the accuracy of the discrimination appeared to have attained an asymptotic level, the birds were given a generalization test during which they were presented with 11 sound intensities in addition to those used in training. Figure 1 shows the generalization test data for the three groups of birds. Note that the proportion of R_2 responses rises gradually with increasing sound intensity, following a curve that is similar to the psychometric function one would obtain from humans tested for intensity discrimination with the method of single stimuli. The birds acted as though they had learned the "rule": make R_1 for soft sounds and R_2 for loud sounds.

Our theoretical account of these data assumes that, during the PSP, the subject learns to "attend" to those sensory channels that provide information predictive of the outcome of its choice behavior. In the experiment we are discussing, for example, the bird learns that of all the stimuli present in the experimental chamber only the intensity of the sound predicts which key choice will lead to reward. Only information arriving over those sensory channels that were found to
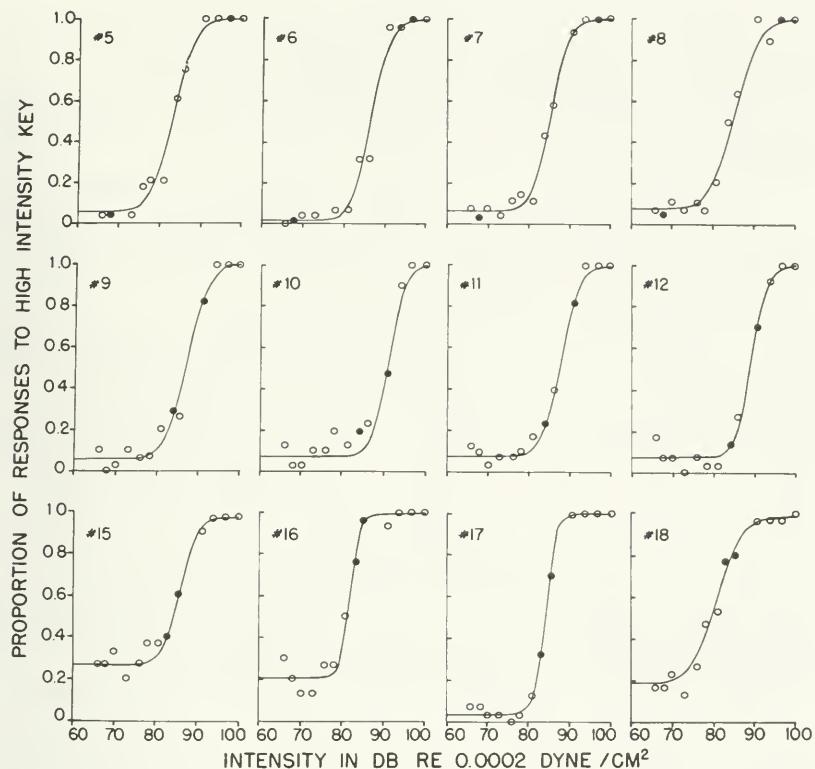
FIGURE 1. Distribution of choices obtained during generalization test following training to discriminate between levels of white noise differing by 29 dB (top row), 7 dB (middle row), and 2.3 dB (bottom row). Each panel shows the results for one pigeon. (From Heinemann, Avin, Sullivan, & Chase, 1969).

transmit information relevant to the discrimination are processed during the second stage of learning.

The second stage of learning involves a memory that has a large but not unlimited storage capacity. This memory will be referred to simply as the *long-term memory* (LTM). On each trial of an experiment the subject is assumed to deposit in the LTM a record that contains:

(a) A representation of the stimulus information that the analysis done during the PSP has shown to provide useful cues. In the example under consideration, the particular loudness experienced when the choice was made is represented as a point on a loudness continuum. The physical differences in the acoustic stimuli determine the separations between the corresponding points along the loudness continuum.

(b) A representation of the response made. For the analysis described here this is represented by a label, e.g. R_1 or R_2.[1]

(c) A representation of the reward received. For the analysis described here the records are labeled as positive if food was delivered; negative if it was not.

Each record is said to occupy a *storage location* in LTM. The location to which each record is sent is selected randomly and any record occupying a storage location will be destroyed ("overwritten") when a new record is entered at that location.[2]

It is assumed that during each trial the subject retrieves from the LTM one or more small random samples of positive records (records showing that a reward was received). Each sample contains from 3 to 18 records. The only information that is used in the response selection process is the information contained in the last sample of records the subject retrieves. After having retrieved a sample, the subject retrieves another sample if, and only if, the sample in hand provides no information about the consequences of past behavior in the presence of sensations reasonably similar to the one currently experienced. Our estimates suggest that, if approximately ten attempts to retrieve useful information have failed, the subject simply chooses the response associated with the largest expected value of reward.

When useable information has been retrieved from LTM, the choice of response is based on a comparison of the information retrieved from the LTM to the sensation induced by activity in the sensory channels to which the subject is attending. This sensation will be called the *current input*. It is assumed that the records of previous sensory experiences are distorted by Gaussian noise while residing in the LTM.[3] After a record has been retrieved, and is being held in working memory, the sensation represented on that record fluctuates rapidly over time, momentary values falling into a Gaussian distribution whose mean represents the value retrieved from the LTM. Four such records are shown in Figure 2.

The response the subject selects is the one that the retrieved information indicates is most likely to earn a reward. To find this re-

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[1]To describe behavior in situations in which response confusion occurs, e.g. when the response keys are closely spaced, responses are represented in memory by stimulation (visual and kinesthetic) received when a particular key was pecked. In such cases key position is represented as varying along a sensation continuum monotonic with key position (see, Chase, 1983).

[2]While this treatment of the LTM is sufficient for the present purposes it is unlikely that the LTM is without organization. As the model develops we plan to consider various sources of organization—temporal, motivational, contextual—and consider how these may interact in the decision processes in which retrieval remains random within the relevant subset of memory.

[3]Without this source of noise all the records in the sample represented by the same response label would be identical. Under these circumstances accuracy of identification would be limited only by sensory overlap.
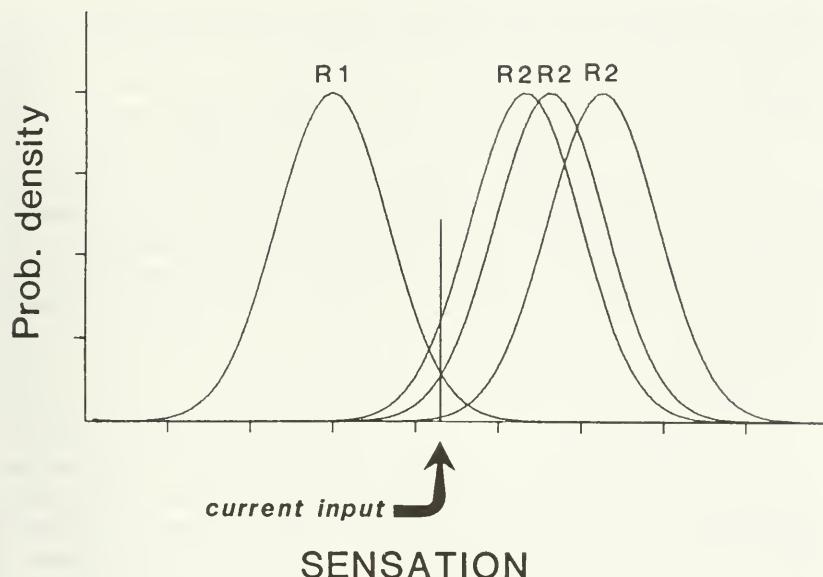
FIGURE 2. A sample of four records retrieved from LTM. The choice of response is based on the probability densities at the point labeled "currrent input."

sponse the subject gets the sum of the probability densities for each response at the current input, and selects the response for which the sum of the densities is the greatest. The process is illustrated in Figure 2, which shows four distributions of remembered sensations, each of which was represented on a single record. Three of the records show that R_2 was rewarded and one shows that R_1 was rewarded. The process amounts to summing the heights of the R_2 curves above the point representing the current input, doing the same for the R_1 curves, and then determining which sum is the larger. The response made is the one for which the probability density is the highest. If the probability density at the current input is below some very small threshold value, a new sample is drawn.

Accuracy is affected by the number of records in the sample that carry the same response label. A correct response cannot be made unless the sample contains at least one record with the required response label. Errors will also be made when the probability density at the current input is highest for an incorrect response. Chase and Heinemann (1991, in press) have shown that, as the number of records associated with each of two responses increases, the effects of the noise added during storage and retrieval from LTM decrease, becoming negligible for sample sizes greater than 32. With a sufficiently

large sample, the only significant source of error remaining is "sensory noise." This is determined by the spacing of the stimuli and may be described as arising from the rapid fluctuation in the sensation represented on that record while it is in working memory.[4]

This model is expressed in the form of a computer program. Precise quantitative predictions are made through presenting the computer with problems and conditions analogous to those presented to our subjects. Computer-simulated performance is compared to the data produced by our subjects. In fitting the data described in this paper all parameters were fixed except (1) sample size and (2) stimulus spacing.

Theoretical Treatment of Generalization

Our model provides the following explanation for the generalization data shown in Figure 1: After training, the LTM is filled with records showing that R_1 was rewarded in the presence of a sensation that was induced by training-stimulus S_1, and R_2 was rewarded in the presence of a sensation induced by training-stimulus S_2. On the average, sensations induced by S_2 will be remembered as more intense than sensations induced by S_1, but the distributions of remembered intensities overlap. Because random samples retrieved from LTM reflect the distribution of records in LTM, it will be true of the sample also that the records showing remembered R_1s will be associated with remembered sensations that are less intense than those associated with remembered R_2s.

As illustrated in Figure 2, the decision rule specifies that the response made is the one for which the probability density at the current input is greatest. Probability densities for R_1 and R_2 tend towards identity at the "category boundary," the point bisecting the distance between the two training stimuli. As the distance from the category boundary increases, the difference in probability densities for the two alternatives increases. As a result, one response in made much more frequently than the other. If this were the only factor operating, the generalization curves would be monotonic and their lower and upper ends would approach asymptotes of 0 and 1.0. However, several experiments have shown that test stimuli that produce current inputs which are far removed from the category boundary may yield response proportions near 0.5, the chance level. According to our model this reflects "guessing", which will occur when repeated sampling has failed to produce useful stimulus information (i.e. a

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[4]The stimuli are represented as points on an axis scaled in standard units. The fluctuations described here as momentary changes in sensation are simply the probability densities defined by the normal distribution.

sample yielding an above-threshold probability density at the current input.)[5]

Effects of Stimulus Complexity

In the Heinemann et al. (1969) experiment the stimuli were sounds that differed in only a single dimension, intensity. The stimuli used in investigations of identification and categorization have ranged from such unidimensional stimuli through multidimensional stimuli and photographs of objects, to the actual objects. In the paragraphs that follow we shall show how the type of stimuli presented influences performance, compare data from a number of different species, and provide a theoretical account of the effects of stimulus complexity on the number of items that can be correctly identified or categorized.

In experiments on identification each stimulus requires a unique response; in categorization the number of stimuli exceeds the number of responses permitted, so that the same response is made for several stimuli. This distinction is not sharp however, because, in practice, it is impossible to present exactly the same stimulus on repeated trials.

The Heinemann et al. (1969) experiment is an example of a two-stimulus identification experiment. During the generalization test novel stimuli were presented for categorization but the subject was not informed whether the category to which any stimulus was assigned was the "correct" one. As shown above, under these conditions the new stimuli appear to be categorized according to the same rule used during identification training. The model treats categorization exactly as it does identification, except that in categorization-training the same response label may be associated with stimuli that differ markedly from each other.

(a) *Unidimensional stimuli.* While a very large number of complex stimuli can be identified without error, humans and other animals are severely limited in their ability to identify stimuli that vary along only a single dimension. In absolute identification situations, stimuli that can be identified perfectly when they are presented in pairs are often confused when they are presented as members of a larger set of stimuli. This rather surprising finding was highlighted in 1956 by George Miller, who pointed out that humans can identify only about "7 plus or minus 2" unidimensional stimuli with perfect accuracy. Much more recently Chase (1983), and Chase, Murofushi,

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[5]In the Heinemann et al. paper (1969) the generalization test data were described using the concepts of signal detection theory. While this theoretical description provides a reasonable first approximation to the data, it requires that the gradients be monotonic. The relationship of the model presented here to signal detection theory is described in Chase and Heinemann (1991, in press).

and Asano (1985) have reported a similar limit in non-human animals.

Figure 3 is an adaptation of the graphical representation Miller (1956) used to show the relationship between information transmitted (number of items correctly identified, expressed as a power of two) and input information (number of equally probable items in the set to be identified). The data shown were obtained from pigeons, humans, and monkeys trained to identify luminance levels that would rarely be confused if they were presented in pairs. The pigeons and monkeys were trained to identify 3,7 or 9 luminance values, covering a range of 3.0 and 3.8 log units for separate groups of pigeons, and 3.2 log units for the monkeys. Also shown is the performance of humans required to identify the 9 luminances used in the monkey experiment. Note that both the monkeys and the pigeons were able to identify three luminance levels virtually without error. As the number of stimuli was increased from 3 to 5 and finally to 9, information trans-
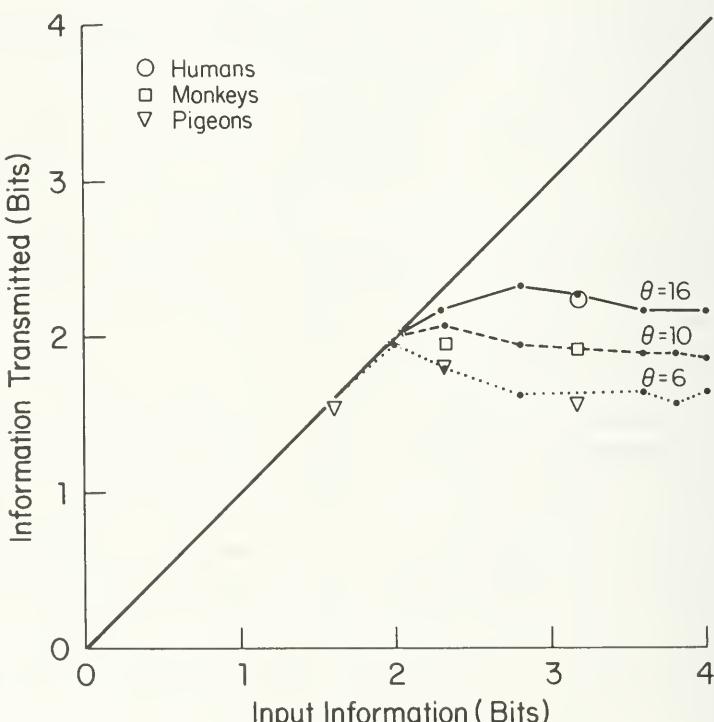
FIGURE 3. Transmitted information as a function of input information. The theoretical curves differ in sample size, θ. Perfect performance is shown by the diagonal line.

mitted remained virtually unchanged for the pigeons. The value was 1.7 bits which is the equivalent of 3.2 items identified without error. Monkeys performed slightly better. For them information transmitted was 2.0 bits, equivalent to 4 items. Information transmitted for the human subjects trained with 9 choices was 2.6 bits, a value close to that suggested by Miller. The lines connecting the dots in Figure 3 are functions predicted by our model.

In order to increase input-information, and thus the potential for correctly identifying more stimuli, additional stimuli must be added to the set. Increasing the number of stimuli within a fixed range decreases the separation between adjacent stimuli. Because most errors involve confusions between adjacent stimuli, it is not surprising that more errors are made as the number of stimuli is increased in this fashion.

However, it might seem reasonable to expect that more stimuli could be identified if the additional stimuli were added at the ends of the range, so that the separation between adjacent stimuli is not decreased. It turns out that increasing the range in this way, or increasing it by increasing the separation between adjacent stimuli, does not solve the problems because the improvement in performance that results from increasing stimulus spacing quickly levels off. This phenomenon, the *range effect*, was first reported for human observers by Pollack (1953) who found little improvement in absolute identification of tones differing in frequency with a 20-fold increase in stimulus spacing. Braida and Durlach (1972) examined performance of human observers in an absolute identification task that involved 10 intensities (equally spaced on a logarithmic scale) of a 1000 Hz tone. As the range of stimulus intensities was increased from .225 to 3.6 log units, performance improved but a further increase in the range from 3.6 to 5.4 log units had little effect on performance.

Similar parametric data do not exist for non-humans. However, Chase (1983) found no differences in information transmitted for pigeons in absolute identification tasks that involved luminance ranges of 3.0 and 3.8 log units. In this experiment separate groups of pigeons were trained with either five or nine stimuli distributed over one of the two ranges. Evidence that pigeons show a range effect was also obtained under different experimental conditions by Richter (1977) and by Hinson and Lockhead (1986).

According to our model, both the range effect and the limit on the number of undimensional stimuli that can be identified without error result from the small number of records held in working memory when the decision is made. Because the size of the sample retrieved from LTM is fixed, each response will be represented by progressively fewer records in the sample as the number of stimuli to be identified increases. For illustrative purposes let us assume that, on each trial

of an absolute identification experiment in which presentation proba-
bilities are equal, a sample of eight records is drawn randomly from
the LTM. In a two-choice situation there will then be, on the average,
four records that provide stimulus information for each of the two
responses. If four responses are possible then each response will be
represented by only two records, on the average. In a situation in
which eight stimuli are to be identified each response will be repre-
sented, on the average, by only a single record. As the number of
responses increases, the amount of stimulus information relevant to
each response decreases. In addition, it becomes increasingly likely
that the correct response will not be represented at all in the sample.
In that situation, increasing the separation between adjacent stimuli
cannot produce any increase in accuracy. Thus, according to our
model, the factor that is responsible for the range effect and the limit
on the number of stimuli that can be accurately identified is the lim-
ited number of records available when the response decision is made.

The deleterious effects of retrieving only a sample of the informa-
tion available in LTM would be diminished if the subject were to re-
trieve more than one sample. However, for resampling to occur the
stimulus to be identified must be very dissimilar from any stimulus
represented in the sample (so that the probability density at the cur-
rent input will be below threshold). This rarely occurs when the ex-
periment is done with stimuli that vary along a single dimension.

In order to obtain the theoretical curves shown in Figure 3, our
computer program made absolute identifications of 3, 5 and 9 items.
In these simulations, the sensations induced by the stimuli were
equally spaced within a fixed range, as was true for the living sub-
jects whose results are shown in Figure 3.[6] The only parameter varied
was sample size. These simulations suggest that pigeons, monkeys,
and humans differ in the size of the sample on which the response-
decision is based. Our simulations yield an estimated sample size of 6
for pigeons, 10 for monkeys, and 16 for humans.

(b) *Multidimensional stimuli.* The number of stimuli that can be
identified without error is larger than seven if these stimuli differ
from each other in more than one dimension. For example, Pollack
and Ficks (1954) found that human subjects could identify without
error as many of 128 auditory stimuli that varied along eight dimen-
sions, such as intensity, frequency, duration, etc. Another example
comes from experiments by Lockhead (1970) who studied identifica-
tion performance of humans in several situations. In one situation
stimuli from two dimensions were presented separately for identifica-

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[6]The stimuli used in training were approximately equally spaced in terms of dis-
criminability. In our computer simulation the extreme stimuli of the set were sepa-
rated by 24 standard units.

tion. In two other situations the stimuli presented for identification were binary compounds created by pairing values from the two dimensions in linear or sawtooth fashion. Lockhead found that the compound stimuli were identified more accurately than their unidimensional components, and, more specifically, that accuracy varied directly with the Euclidean distance between pairs of adjacent stimuli. Chase and Heinemann (1972) published data showing that this was true for pigeons as well.

We use the Euclidean metric in our theoretical treatment of identification of multidimensional stimuli. We assume that each sensation is represented by a point in n-dimensional space and the distributions representing remembered sensation are n-variate Gaussian ones. Increasing the dimensionality of the stimuli increases the Euclidean distance between remembered sensations. In addition to improved discrimination, this results in an increase in the number of trials on which resampling occurs. Both factors appear to be responsible for the improvement in accuracy as the dimensionality of the stimuli increases. For example, in our simulations of the Pollack and Ficks (1954) experiment, the current input corresponding to each eight-dimensional space, and each remembered value of such a current input is represented by an eight-dimensional Gaussian distribution. Under these conditions a larger number of stimuli can be identified without error because of the geometric fact that the distance between the peaks of distributions that represent remembered values of the stimuli increases with the dimensionality of the space. The greater geometric distance among stimuli results in substantial resampling because, in the eight dimensional space, the sum of the probability densities is quite frequently below threshold at the current input. The results yielded by the computer program are identical to the empirical results of Pollack and Ficks.

(c) *Patterned stimuli.* The improvements in performance that result, empirically and in theory, from increasing the number of redundant cues on which identification is based is relatively small when one considers the fact that many thousands of complex stimuli such as faces, pictures, spoken words, and Chinese characters can be identified virtually without error by humans. As noted by Lockhead (1970) "the judging of multidimensional aspects of a complex stimulus is not sufficient to account for the large number of objects we can identify in the world."(p. 8) He showed that even simple patterns, 20 face-like patterns composed of four lines within a circle, could be identified without error.

According to our model the increase in the number of complex stimuli that can be identified without error results primarily from resampling.

In situations in which spatial information is irrelevant, as is true

for sounds or an evenly illuminated surface, we treated sensory information as though it arrived over a single "sensory channel." In extending our model to visual pattern recognition we assume that at any moment in time the continuum of sensations induced by a pattern of stimulation may be represented by a sample of evenly spaced "sensory channels." That is, in representing visual patterns the internal representation of the visual field is partitioned into finite-sized cells called pixels. Each pixel is characterized by its two spatial coordinates and its hue, saturation, and brightness. Any particular visual experience can be represented in memory by the spatial coordinates of the relevant channels, and codes for the brightness, hue, and saturation at each channel.

In our simulations of pattern recognition we have so far considered only dot-matrix patterns made up of two gray-levels, e.g. black points on a uniform white background. This simplification makes it unnecessary to represent the non-spatial dimensions. It is assumed that while a record of a visual pattern resides in LTM, the values of the X and Y coordinates of each point vary randomly and independently over time, the distributions of momentary values being Gaussian. A record of this type is illustrated in Figure 4. The concentric circles represent the bivariate density functions representing the remembered letter A. The x's represent the current input points produced by the dot matrix letter A.

According to our model, a subject trained to recognize a number of different dot matrix letters when shown a particular letter for identification, retrieves a few records from LTM and compares the current input pattern to each of the patterns represented on the retrieved records in order to find the best match. We assume that response selection is based on a decision quantity D, computed as follows: At each point on the current input calculate the mean probability density contributed by each point on the memory record. (A mean density that falls below the threshold is assigned a value of zero.) This will yield as many means as there are current input points. The decision quantity, D, is equal to the product of these means. If two or more records in the sample represent the same response, the value of D associated with that response is the sum of the individual D values. The decision rule is: Make the response associated with the largest value of D. If no record is associated with a value of D that is greater than zero, draw a new sample. Finally, if k successive samples fail to yield a non-zero value of D for any record, then choose the response associated with the greatest probability of reward in the past. This rather complicated-sounding procedure is simply an extension of the decision rule described earlier for the treatment of unidimensional stimuli. It is a type of "fuzzy template" matching scheme in which the current input (a pattern) is compared to remembered patterns. The
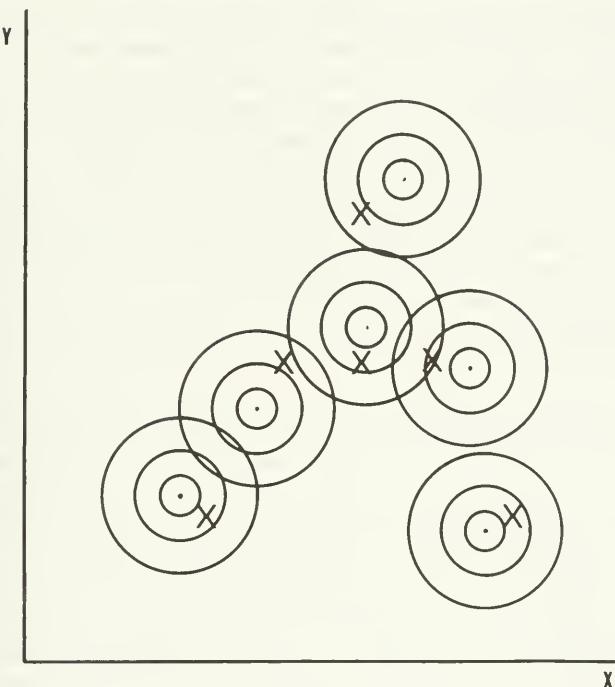
FIGURE 4. Remembered group of points representing the letter A as shown on a single record retrieved from LTM. The concentric circles represent contours of constant probability density on the bivariate distributions for the spatial coordinates of each point. The x's represent points on the current input.

response made is the one associated with the greatest probability of being correct.

The model was used to simulate choice behavior in a pattern recognition experiment involving the 26 letters of the alphabet. The confusion matrix generated showed that certain errors, e.g., confusions between E and F will occur frequently while others, e.g., A and T rarely occur. The simulated matrix compared quite well with one published by Blough (1985) which was based on confusions made by pigeons presented with the same stimuli in a three-choice discrimination task (Heinemann & Chase, 1990). The model-generated confusion matrix also correlated well with one based on confusions made by a chimpanzee who identified the letters by pressing a key on a console (Matsuzawa, personal communication), and with matrices based on human reaction times and similarity ratings (Podgorny and Garner, 1979).

It was pointed out earlier that humans can identify a vast num-

ber of patterned stimuli. The ability to identify large numbers of complex stimuli is clearly not uniquely human. Pepperberg's (1981) parrot made a different vocal response to each of more than 50 objects. Terrace (1979), following the earlier work of Gardner and Gardner (1978), trained a chimpanzee to express over 125 words in American Sign Language. Other researchers (e.g. Asano, Kojima, Matsuzawa, Kubota & Murofushi, 1982; Premack, 1976; Savage-Rumbaugh, 1984) trained chimpanzees to identify objects by touching or manipulating forms that represented these objects. Although, it is beyond the scope of this paper to consider whether the behavior observed in these animals is evidence of linguistic abilities, these studies do provide evidence that non-humans are capable of identifying many stimuli.

Although pigeons can be trained to choose among as many as nine response keys (Chase, 1983), most research on pigeons' memory for complex stimuli has examined categorization rather than identification. The ability of pigeons to categorize an amazingly large number of colored photographs on the basis of rote memory was first demonstrated by Greene (1983) and Vaughan and Greene (1984). For example, Vaughan and Greene (1984) trained pigeons to memorize, by rote, more than 300 scenes projected in full color. In this experiment pecking on some randomly selected photographs was rewarded, pecking on others delayed the end of the trial. Pigeons learned this task readily and showed excellent retention when tested later. In a related experiment, Heinemann, Ionescu, Stevens, and Neiderbach, (in preparation) showed pigeons slides of natural scenes projected on a small screen located between two choice keys. The pigeons were rewarded for pecking either the left of right choice key. Half of all pictures shown were randomly assigned for reward if the right key was pecked, the other half for reward if the left key was pecked. During the course of the experiment the number of pictures presented was increased in rather large steps from 80 to 640, at which point the pigeons were performing at a level of about 85 percent correct. Although the experiment was terminated at that point, there was no evidence that the pigeons were approaching a limit on the number of slides they could categorize.

CONCLUSION

The data presented here suggest that the processes underlying identification and categorization are similar in humans and non-humans. Preliminary work suggests that the number of remembered items that can be held in working memory varies among species. However, the number of stimuli that can be identified or categorized appears to depend much more upon the characteristics of the stimuli

than upon the organism making the identification. Both humans and non-humans are severely limited in their ability to identify stimuli that vary along a single dimension. Increasing the dimensionality of spatially undifferentiated stimuli (e.g., evenly illuminated areas of constant shape) improves performance. However, this improvement is trivial compared to that observed when spatially complex stimuli, such as pictures, are presented for identification.

In dealing with visual patterns our model represents the spatial aspects of the visual sensations as sensory channels or pixels whose spatial coordinates can be defined in a two-dimensional space. The basic processes involved in the identification of such complex stimuli are assumed to be the same as those involved in identification of uni-dimensional ones: A small sample of records is drawn from long-term memory. The pattern of stimulation represented on each of these re-cords is compared to the current pattern of stimulation. If a reason-able match is obtained, that is, if the joint probability density associ-ated with the current input (D) is above threshold for at least one of the records, then a response is made. If none of the comparisons yields a value of D that is above threshold then a new sample is drawn. Additional samples are drawn until a match (or a guess if sampling fails to retrieve useful information) is made.

This description of identification and categorization is, of course, based on a variety of simplifying assumptions. For example, in its present state of development our model treats visual patterns as "snapshots", whereas living organisms looking at real objects are al-most invariably exposed to patterns of stimulation that are continu-ously changing because of movement of the object that is being in-spected, or of the inspecting organism. Further development of our model will depend in part on the removal of some of these simplifying assumptions. Much additional work, both theoretical and empirical, is needed before the fine differences and similarities among species are understood. Many alternative theoretical approaches to the prob-lems that have been discussed are obviously possible, but very few have been developed in quantitative detail. If the heavy theoretical emphasis of this paper needs any justification, it is that any compara-tive analysis of psychological *processes* is necessarily bound to theory.

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